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CONTENTS

The statistical outlook in relation to ecology. By C. B. WILLIAMS

Life between tide-marks in North America: III A. Nova Scotia and Prince Edward Island: description of the region. By T. A. and ANNE STEPHENSON

Life between tide-marks in North America. III B. Nova Scotia and Prince Edward Island: the geographical features of the region. By T. A. and ANNE STEPHENSON

Studies of the development of woodland conditions under different trees. II. The forest floor. By J. D. OVINGTON

The influence of 'midnight sun' conditions on certain diurnal rhythms in *Oxyria digyna*. By J. WARREN WILSON

On the interpretation of the discontinuous distributions shown by certain British species of open habitats. By C. D. PIGOTT and S. M. WALTERS

Stratigraphy and pollen analysis of Southern Pennine blanket peats. By VERONA M. CONWAY

The significance of large pH fluctuations observed in some South African vleis. By K. H. SCHÜTTE and J. F. ELSWORTH

The seasonal cycle of the plankton diatom, *Melosira italica* (Ehr.) Kütz. subsp. *subarctica* O. Müll. By J. W. G. LUND

A study of the relation between growth form and exposure on Monte Maiella, Italy. By F. H. WHITEHEAD

Studies in the quantitative morphology and ecology of *Eriophorum angustifolium* Roth. II. Competition and dispersion. By MARIE E. PHILLIPS

The vegetation of sugar-cane flood fallows. By D. B. FANSHAWE

Locating strata in tropical rain forests. By I. V. NEWMAN

Reviews

Biological flora of the British Isles: Deschampsia flexuosa (L.) Trin. By G. Scurfield. *Viola lutea* Huds. By O. E. Balme. *Arum neglectum* (Towns.) Ridley. By C. T. Prime. *Colchicum autumnale* L. By R. W. Butcher

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POPULATION FLUCTUATIONS IN SOME NORTHERN HEMISPHERE GAME BIRDS (TETRAONIDAE)

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(With 6 Figures in the Text)

CONTENTS

	PAGE		PAGE
INTRODUCTION	1	GREENLAND	17
SPECIES STUDIED	1	ICELAND	17
RECORDS USED	2	BRITISH ISLES	19
METHODS OF ANALYSIS	3	NORTH-WESTERN EUROPE	20
MAIN CANADIAN AND U.S.A. FLUCTUATIONS 1924–25 TO 1950–51	5	SOVIET RUSSIA	23
		SPITSBERGEN	24
POPULATION FLUCTUATIONS BEFORE 1924–25	12	DISCUSSION	25
NEWFOUNDLAND AND THE MARITIME PROVINCES	13	ACKNOWLEDGEMENTS	27
		SUMMARY	27
ALASKA	15	REFERENCES	28

INTRODUCTION

So much has been written on population fluctuations in Northern Hemisphere game birds that to add further to an already overburdened literature requires some justification. This paper is offered with the excuse that it makes available a large amount of material—hitherto untouched—on various species of Tetraonidae in North America, this material being incorporated in various records lodged with the Bureau of Animal Population at Oxford; and included for the first time in such a review as this is recent information relating to the tetraonid populations of Iceland, Spitsbergen and the north-western U.S.S.R.

The paper has been designed to find out: first, whether the game-bird cycles are synchronous throughout North America; and secondly, whether the cycles described for the Old and New Worlds are synchronous or of different periodicity. Finally, it is hoped that useful information will have been provided for those undertaking a study of the relationships between these game birds and other cycle species.

SPECIES STUDIED

The present paper deals primarily with population fluctuations in the genera *Lagopus* and *Bonasa* in North America and with *Lagopus* in other parts of the Northern Hemisphere. Another North American species that is frequently mentioned is the sharp-tailed grouse, *Pedioecetes phasianellus*.

Four species of *Lagopus* are now recognized in the Holarctic (Peters 1934), three of which occur in North America: the rock ptarmigan, *L. mutus*; the willow ptarmigan (less correctly but more commonly called willow 'grouse'), *L. lagopus*; and the white-tailed ptarmigan, *L. leucurus*. Each of these is divided into several subspecies, but the

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details of these need not concern us here. The rock ptarmigan has the most northerly—mainly Arctic—distribution, being gradually replaced farther south by the willow ptarmigan; and the white-tailed ptarmigan is roughly confined to the Rocky Mountain system from Alaska to New Mexico (Taverner 1926). The rock and willow ptarmigan are migratory—the behaviour of the latter species being much more obvious than that of the former in this respect, since it may appear at low altitudes well south of the tree-line in winter.

In Greenland and Iceland only *L. mutus* occurs (Salomonsen 1951), but in northern Europe and Asia both *L. mutus* and *L. lagopus* are found and in much the same relation to each other as in North America except that *L. mutus* also occurs in the Alps and some other southern mountain ranges. Once again, there are several subspecies.

Two species occur in the northern British Isles—*L. mutus*; and the 'red grouse', *L. scoticus* of which there are two subspecies (Vesey-Fitzgerald 1946).

Bonasa umbellus, the ruffed grouse, has had up to 12 subspecies described (Snyder & Shortt 1946). It is confined to North America and, being a dweller in deciduous and mixed forests but avoiding purely coniferous areas, it is found south of the tree-line from Alaska right across the continent to south-eastern Labrador. Its range extends into the U.S.A.—especially in the north-central and north-eastern states (Bump *et al.* 1947); thus its geographical distribution overlaps to some extent with that of ptarmigan although its normal habitat is different. It is non-migratory.

The sharp-tailed grouse, of which there are three subspecies, has a geographical distribution similar to that of the ruffed grouse, except that it is not generally found to the east of Hudson Bay or in the north-central or eastern United States (Trippensee 1948). It is a bird of marginal lands rather than true forest or well-farmed country and occasionally undertakes fairly extensive migrations—especially at times of great abundance (Snyder 1935). This species is sometimes miscalled 'prairie chicken'—a name pre-empted by *Tympanuchus cupido*.

A number of other game-birds are dealt with in brief during the course of this paper, but it is not necessary to discuss them in any detail here.

RECORDS USED

For the construction of the graphs showing the fluctuations in *Bonasa* and *Lagopus* in Canada from year to year three sources of information have been used:

(i) The annual zoological reports of the Hudson's Bay Company 1924–25 to 1950–51 (there are no records for the year 1931–32).

(ii) The annual reports of the Canadian Arctic Wildlife Enquiry 1934–35 to 1948–49.

(iii) The annual reports of the Biological Board of Canada (referring to New Brunswick, Nova Scotia and Prince Edward Island only) 1932–33 to 1939–40. Details concerning the origin and sponsoring of these enquiries may be found by consulting Chitty (1948, 1950*b*).

For most years the informant was asked to state the area to which his reply referred, to compare the abundance of the bird in question with that of the previous year both in the breeding and non-breeding seasons, to record, if applicable, whether there had

been any unusual migration and when this had occurred, and finally to report on any epidemic. The year referred to throughout is the one ending on 31 May. Occasionally the phrasing of the questionnaires was varied slightly and information on all species was not always asked for. Thus for the first three years, 1924–25 to 1927–28, only 'willow grouse' was included in the forms; then for about eleven years 'ptarmigan', 'ruffed grouse' or 'grouse (partridge)' were listed. Next followed a spell of five years when there were separate sections in one questionnaire or another for 'rock ptarmigan', 'ruffed grouse', 'willow ptarmigan' and 'other grouse', followed by a period of reversion to forms listing only 'grouse' and 'ptarmigan' and so on. At times some reporters included data on such species as spruce grouse (*Canachites canadensis*), prairie chicken and Franklin's grouse (*C. franklinii*)—but this was relatively uncommon.

METHODS OF ANALYSIS

The material from the above sources has been treated comparatively in the following manner. In so far as the phrasing of the individual reports makes it possible, without in any way doing violence to the original opinions expressed, the information each contains has been classified under one of the following groups: 'increasing', 'no change' and 'decreasing'—each of which may in turn be qualified by one of the alternatives: 'abundant', 'normal' and 'scarce'. No discrimination has been made between the various degrees of abundance and scarcity, as this is of little value and 'abundant' has been taken as equivalent to 'plentiful', 'very common', 'numerous' and so on; and 'scarce' has been regarded as synonymous with 'few', 'occasional', 'almost none', etc. A small proportion of the total number of replies from all sources give 'none' as an answer without any further qualification. These have not been included in the analysis because of the difficulty of appraising the real significance of the reply in a number of instances: but a remark such as 'none this year' is regarded as another variation of 'scarce'. Although in any one year there have sometimes been conflicting reports about the same area, no attempt has been made to reconcile these or to discriminate between them—the original evidence is presented with as little distortion as possible. The reports on each species for each year have been entered within a grid system similar to that used by Chitty & Elton (1938) in the snowshoe rabbit enquiry; except that, as a consequence of there being a much smaller number of observers in the present investigation, the grid units employed have been squares of 300 miles a side instead of 30 (see Fig. 1).

For any one year the difference between the percentage of the total number of replies that state that the species is either increasing or unchanged in numbers but abundant, over those reporting a decrease or unchanged scarcity, has been calculated and used as the data from which has been found by plotting the figures for successive years the '*final year of abundance*' in an area. (When these two percentages added together do not make up 100%, the difference is composed of those replies stating 'normal' or 'no change'. Replies stating 'abundant' or 'scarce' without qualification have not been used.) The final year of abundance, which by implication immediately precedes the crash, has been used to fix the periodicity and dating of the cycle because it is felt that, being at a point of great relative change, it is a much more obvious and reliable landmark than the *year of peak abundance* (with which it frequently, but not always,

coincides) so often used in studies of this kind, and which in any case is not easy to determine precisely even in a restricted area. However, the inherent difficulty in this method is in supplying a consistent and satisfying definition of what is meant by a 'crash', for it will be obvious that the standards accepted in this paper are very different from those used by, say Siivonen (1948). A hard-and-fast definition is difficult, if not impossible, to give, but I have been guided by the following criteria: There must be a sharp and sustained fall of considerable magnitude within one or

Fig. 1. The distribution of reporting Hudson's Bay Company posts and the grid system used in analysing questionnaire returns.

more years (in practice it is generally found to be more than one) from a peak of abundance higher than the average shown in the curve, and this in turn should have been preceded by a rising tendency or a period of relative abundance of more than a year's duration. I have also used these considerations as a guide in my interpretations of other authors when the conclusions I have reached differ in any marked degree from their own.

If for no other reasons than because of the way the questionnaires have been phrased from time to time and because of the rather confusing popular synonymy for many of these game birds in North America, it is certain there has been some lack of discrimination in the reports occasionally between ruffed grouse, willow 'grouse', sharp-tailed grouse and spruce grouse, etc., on the one hand, and rock ptarmigan, willow ptarmigan and sometimes, no doubt, white-tailed ptarmigan on the other. From a study of the known geographical ranges and ecological preferences of the various

species it is possible in many of the doubtful cases to effect a separation, especially when dealing with the more extreme parts of the respective ranges. But a number of instances remain in which one cannot be sure what species is being referred to. However, in nearly all years in which the questionnaires or the reporters do specify particular species, there are frequent indications that the fluctuations tend to occur in synchrony. This impression is given support from the literature—as will be shown later. In this section of the paper, however, since the great majority of the replies obviously refer either to the ruffed grouse or the rock and willow ptarmigan, any distinctions that are made will be made as between the genus *Bonasa* and the genus *Lagopus* as a whole; and, except where it is obvious to the contrary from the context, all references in the questionnaires to 'grouse' and 'partridge' have been taken to refer to ruffed grouse, and all references to 'willow grouse', 'white partridge' or 'ptarmigan' have been taken to refer to the genus *Lagopus*.

Only reports applying to each year as a whole have been used in the quantitative analysis, for although many of the earlier questionnaires asked for separate comments on the breeding and non-breeding seasons, most were in agreement for both these periods, especially those concerned with ruffed grouse, but some of the reports on ptarmigan refer to migration movements and these may possibly have given rise in some cases to false ideas of abundance or scarcity. Therefore all records that show disagreement between breeding and non-breeding seasons or refer to only part of the year have been disregarded. The number that have had to be rejected for these reasons is very small and their absence in no way biases the results. To the question whether epidemics were noticed at the times of population crashes, when answers were given they were, with one exception, always in the negative. On the question of the justification for this method of treating the raw data and the likelihood of its proving reliable one can say only this: Relying as it does on observers of all standards of ability some of whom have lived for only a short time in the area they are reporting on, and dealing as it must with only general trends in a very complex phenomenon, it is not claimed that the questionnaire method is the ideal one for studying population fluctuations; in fact, in dealing with the Tetraonidae where the difference between the maximum and minimum population densities is very much less marked than is the case with the smaller mammals—as Lack (1951) has also pointed out—it leaves much to be desired. Nevertheless, if used with discretion and in conjunction with other methods or with the reports of trained observers of recognized reputation, it is a most valuable tool. Mention of ruffed grouse or ptarmigan fluctuations in the Canadian Snowshoe Rabbit Enquiry questionnaires and in the literature have not been treated quantitatively with the main body of data because, being occasional, these reports may be biased since it seems reasonable to assume that they are more likely to appear at times of unusual abundance or scarcity.

MAIN CANADIAN AND U.S.A. FLUCTUATIONS, 1924–25 TO 1950–51

We will deal first with the results obtained from the annual reports of the Hudson's Bay Company and the Arctic Wildlife Enquiry. The Biological Board of Canada reports which are the sole source of quantitative data for the Maritime Provinces will be discussed in a separate section.

By use of the grid system attempts were made to establish whether there was any time gradient in the onset of the crashes (either radiating from a centre or spreading across the country in a particular direction), or whether some areas *consistently* experienced crashes before or after others. All attempts to demonstrate such effects were unsuccessful—either between individual squares or between combinations of blocks of squares. Differences were found, of course, but these were not consistent; and with single squares the number of entries in each was usually not great enough to permit reliable comparisons being made. When areas were taken such that the number of entries was enough to allow of some confidence being placed in the comparisons, differences in most cases did not appear to be significant. Therefore the data for the ruffed grouse or ptarmigan will be presented as applying primarily to Canada as a whole (with the exception of the Maritime Provinces, as already stated). Furthermore, when the number of records compared in each case were great enough to give confidence in the results, there did not seem to be any well-marked difference between the dating or periodicity of the cycles of the various *species*; although, as will be seen, the years 1936–37 and 1937–38 appear to be exceptional in this.

Although the records begin with the year 1924–25 it is not until 1927–28 that they become numerous or representative enough to be treated quantitatively with any assurance. Of the thirty-four replies to the Hudson's Bay Company questionnaires in that year only five stated that grouse or ptarmigan numbers were increasing or unchanged-abundant and twenty-seven told of decrease or continuing scarcity (Table 1). But if there is a shortage of Hudson's Bay Company reports for these early years there are numerous references in the literature to the widespread scarcity of the birds at that time. Taking these reports by district or province we find that for Labrador, Lewis (1928) and Strong (1930) between them refer to the virtual absence of rock and willow ptarmigan and spruce grouse during the winter of 1927–28; for Ontario, Bensley (1928), Fairbairn (1927), Fargo & van Tyne (1927), Mitchell (1929) and Snyder *et al.* (1928) all refer to much-diminished ruffed grouse populations in various years between 1924 and 1928; for Manitoba, Criddle (1930) shows that both ruffed grouse and sharp-tailed grouse were experiencing a crash about this time; for Alberta, similar statements about ruffed grouse occur in Hayden (1928), Lawton (1927), Randall (1926) and Rowan (1925); and for British Columbia, Mailliard (1932) found ruffed grouse scarce in the Kootenay Valley in the spring of 1928.

There are reports of scarcity in Canada as a whole in Rowan (1926) and Taverner (1929); yet in the midst of this great dearth there were occasional exceptions to be found: Calvert (1925) states that ruffed grouse were common in the Lindsay district of Ontario in that year, and Rowan (1926) remarks that this species was locally abundant at Athabaska Landing and Lake Labiche, Alberta. In the Northwest Territories Critchell-Bullock (1931) found willow ptarmigan abundant about Artillery Lake but scarce along the Thelon River and rock ptarmigan common throughout the winter of 1924–25. Beyond Canada, in the northern United States, a widespread scarcity is reported for the years 1925–28. Fisher (1939) may be consulted for Michigan, Green (1932) and King (1937) for Minnesota, and Bump (1939) for a more general account covering many states.

Fig. 2 shows that recovery was rapid throughout Canada, especially after 1927–28,

and this has been commented upon in various ways by many authors—for parts of Ontario by Bates (1929*a*, *b*), Fairbairn (1930) and Snyder (1938), and for Manitoba by Criddle (1930). In south-western Saskatchewan, Potter (1930) reports an increase

Table 1. *Annual reports of population changes in some species of Canadian tetraonids*

	Ruffed grouse Hudson's Bay Company reports and Arctic Wildlife Enquiry Reports				Rock and willow ptarmigan Hudson's Bay Company reports and Arctic Wildlife Enquiry Reports				Ruffed grouse Maritime Provinces only (Biological Board of Canada) Reports			
	Total no. of reports	Total reports of increase and unchanged abundance	Total reports of decrease and unchanged scarcity	Percentage excess of col. 3 over col. 4	Total no. of reports	Total reports of increase and unchanged abundance	Total reports of decrease and unchanged scarcity	Percentage excess of col. 7 over col. 8	Total no. of reports	Total reports of increase and unchanged abundance	Total reports of decrease and unchanged scarcity	Percentage excess of col. 11 over col. 12
1924–25	—	—	—	—	16	4	11	−44	—	—	—	—
1925–26	—	—	—	—	18	1	15	−77	—	—	—	—
1926–27	5	0	5	−100	17	4	13	−52	—	—	—	—
1927–28	19	3	14	−58	15	2	13	−74	—	—	—	—
1928–29	21	8	12	−19	17	8	7	+6	—	—	—	—
1929–30	44	25	15	+23	25	9	11	−8	—	—	—	—
1930–31	37	30	4	+70	31	22	5	+55	—	—	—	—
1931–32	—	—	—	—	—	—	—	—	18	7	9	−11
1932–33	9	8	1	+77	7	4	3	+14	25	8	15	−28
1933–34	82	23	45	−27	6	5	0	+83	9	2	7	−55
1934–35	74	16	50	−46	6	1	5	−66	20	11	6	+25
1935–36	92	19	64	−49	102	22	62	−39	22	13	5	+36
1936–37	103	21	67	−45	43	26	9	+39	19	14	3	+58
1937–38	105	40	48	−8	50	36	6	+60	20	18	0	+90
1938–39	104	34	33	+1	261	97	94	+1	25	24	0	+96
1939–40	101	34	27	+7	267	103	86	+7	21	16	4	+57
1940–41	104	23	34	−11	280	103	79	+9	—	—	—	—
1941–42	108	23	35	−11	176	61	57	+3	—	—	—	—
1942–43	103	12	46	−33	220	34	113	−36	—	—	—	—
1943–44	8	1	6	−54	82	14	51	−45	—	—	—	—
1944–45	99	11	63	−52	139	27	83	−41	—	—	—	—
1945–46	104	15	63	−48	138	35	74	−29	—	—	—	—
1946–47	99	14	46	−32	122	25	64	−32	—	—	—	—
1947–48	101	44	31	+13	118	36	44	−7	—	—	—	—
1948–49	93	53	13	+43	105	44	26	+17	—	—	—	—
1949–50	91	44	15	+31	—	—	—	—	—	—	—	—
1950–51	76	19	28	−12	—	—	—	—	—	—	—	—

in ruffed grouse in 1929, and Lawton (1929) and Rowan (1929) do the same for Alberta —the former referring to ruffed grouse, the latter to spruce grouse. Fairbairn (1931) found ruffed and spruce grouse common near Dawson's Landing in the Northwest Territories in September 1929, and even 2 years earlier it was evident that the tide was beginning to turn in this area for ruffed grouse at least (Rowan 1927). In a paper on the sharp-tailed grouse, Snyder (1935) gives an account of population variations of this species in widely separated areas of Canada showing that there was a general tendency for an increase in its numbers at this time following upon an equally general low about 1926. Gross (1931, 1932), as well as some of the authors already cited in connexion with the northern United States, may be consulted for details of the ruffed

grouse cycle of about this time in the north-east U.S.A.: marked decreases in the New England states became noticeable after 1923 and there was a general scarcity in 1925–26 after which numbers steadily increased. Thus it is apparent that the pattern of change in this area bears a close resemblance to that just described for much of Canada and is indeed an obviously integral part of it.

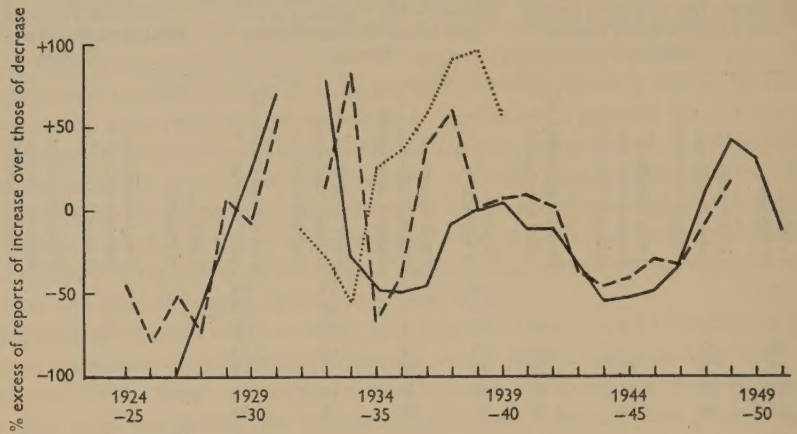

Fig. 2. Population fluctuations in Canadian tetraonids compiled from various annual reports (see Table 1). ——, ruffed grouse (Hudson's Bay Co. and Arctic Wildlife Enquiry); – – –, rock and willow ptarmigan (Hudson's Bay Co. and Arctic Wildlife Enquiry); ..., ruffed grouse in Maritime Provinces.

From Table 2 it is clear that the final year of abundance for the various tetraonids in North America (outside of Alaska and the Maritime Provinces) fell mainly between 1932–33 and 1933–34. The table presents in graphic form the fact that a good number of widespread and independent observers in parts of the country, not covered by the Hudson's Bay Company reports, agree on this. A notable feature of the time was the great willow ptarmigan invasion of the winters of 1932–33–34. This became more extensive each year and extended finally from central Alberta in the west to southern Quebec in the east. In the summer of 1934, Dalgety (1936) found rock ptarmigan common in the Cape Christian–Eglinton Fiord area of Baffin Island; and far to the south in the central United States, Schwartz (1945) fixes 1933 as the final year of abundance for prairie chicken in Missouri.

Comments included in the Canadian Snowshoe Rabbit Enquiry and the Arctic Wildlife Enquiry questionnaires are valuable: first, because they afford a check from yet another source than the scientific literature on our figures; and secondly, because they supply information about areas not otherwise covered. For instance, the 1933–34 returns of the Snowshoe Rabbit Enquiry include twenty-six reporting on ruffed grouse and ptarmigan, and of these sixteen state that there had been an increase and ten a decrease. For 1934–35 there were twenty references of which only four were of increase—the remainder being of decrease. (The few reports about the Maritime Provinces for these 2 years—four in all—have not been included here.) The Arctic

Table 2. *Peak years or final years of abundance for individual grid squares (see Fig. 1). Liter*

* Ruffed grouse. † Ptarmigan. § Other tetraonids. [ ] Ruffed grouse in the Maritime Provinces. Superscript numb
C, reports from the Arctic Wildlife Enquiry; D, reports fr

	1	2	3	4	5	
H		†1934[C] †1941[A]				
G	*1915[8] †1935[C] †1943[39a, A]	†1932[C] †1934[C] †1943[A]			†1904[2a]	
F		†1934[B]	†1940[A]			
E	*1932[11] *1950[A]	*†1942[A]	*§1934[B] †1939[A] *1949[A]		†1933[C]	
D	§1911[47] §1923[47] *1932[8, 33, 38, 39] *1942[39]	*1893[8] *1896[42] *1906[42] *1915[42] *1916[8] *1922[8] *§1925[42] *§1932[40] *§1933[8, 43, 47] *†1934[19, 42] *1937[50] *†§1942[42, 44] §1943[7] †1950[44]	*1904[8] *1916[8] *1922[8] *§1932[8, 47] *†1939[A] *1941[B] *1950[A]	§1933[47] †1941[A]	†1934[1, 2, B] †1942[A]	
C	*1948[29]	§1943[7]	†1935[37] *1939[37] §1942[7]	*1922[4, 8] *1932[8] *1933[4] *1934[46] *†§1935[10, 41] *§1942[4, 7, 39]	*1902[8] *1913[8] *1923[8] *§1933[8, 47] †1934[13] †1942[A] *1949[A] †1950[13]	
B				*§1904[12] §1913[12] *1915[12] *1924[12] §1925[12] *1942[38]	*1905[14] *1914[14] *1915[8] *§1923[47, 48] *1924[8, 14] *1932[26] *§1933[14, 32, 47] *1934[8, 35] *1941[18] *1942[14] *1943[35]	*190 *191 *192
A					*1898[45] *1906[14, 45] *1914[14] *1924[14] *1933[14, 31] *§1934[24, 45] *§1942[24, 31] *1943[45]	*190 *191 *192 *192

e reports have been placed in those squares to which they apply or mainly apply

fer to the bibliography. A, results from grid plotting; B, reports from the Snowshoe Rabbit Enquiry; he Biological Board of Canada Enquiry.

	†1938[A] †1941[A]				
			†1943[28]		
JDSON					
	†1933[5]		†1933[5]	†1905[6a]	*†1933[A] †1939[A] *†1945[25, A]
BAY					
*†1940[A] *1941[18] *1950[A]	†1934[B] †1941[A] *1950[A]	*1906[8] *1923[8]	*1933[8] †1941[A]	†1895[9] †1904[9]	*1932[33]
*1932[8] †1934[B] *1935[A] *1941[18]	*1924[49]	*1933[34] *1934[34] *1940[18, A] †1942[B]	*1906[14] *1915[14]	*†1933[14, 15, 23] *1935[14]	*1895[6] *1905[6, 14] [1912[D]] *1915[14] *1923[6, 14] [1922[51]] [1923[14]]
*1932[14] *1942[14, 15]	*1905[8] *1906[14] *1913[8] *1914[14] *1923[8, 14, 27]	*1933[8] *1935[14] *1942[14] *1952[21]	*1906[14] *1914[11] *1915[14] *1923[14] *1925[27]	*1933[14] *1935[14] *1942[22]	

6	7	8	9	10

Wildlife questionnaires (1935–40) contain ten references to the years 1932–35. Of these, eight deal with the Yukon–Great Bear Lake–Mackenzie Delta region and all state that the years of abundance lay between about 1932 and 1934. The other two comments are upon the Chesterfield Inlet–Nueltin Lake–Nonala district of western Hudson Bay and fix 1932–33 as the last period of abundance. A typical comment is as follows:

> 1933–34: Central Alberta, from Edmonton north about 100 miles....Grouse generally have been more plentiful than for the last 10 years but have disappeared almost completely to the north, in several districts preceding the 'crash' of the rabbits....Ptarmigan have come south in large numbers. (W. Rowan.)

From Fig. 2 it can be seen that a general crash occurred between the years 1933 and 1935 and that the last year of dearth was 1935–36. This period of scarcity is widely reported in the literature; e.g. for ruffed grouse in Haliburton County, Ontario, by Mitchell (1937), for a number of species in Alberta by Rowan (1948), and for willow ptarmigan in the Foxe Basin area, Northwest Territories, by Bray (1943). This author states that rock ptarmigan were plentiful during spring migration in the same year, 1937; but, as previously remarked, reports of migration flocks may give false ideas of population trends unless the observer has remained in the area for at least one season beforehand. In the United States, Grange (1949) demonstrates synchronous 'lows' for ruffed grouse, prairie chicken and sharp-tailed grouse about this time in Wisconsin, and King (1937) and Green, Evans & Larson (1943) report a scarcity of ruffed grouse in Minnesota.

Now follows the usual period of recovery, and reports of fair or increasing numbers of ruffed grouse or ptarmigan during the years 1937–40 may be found in Brown (1947), Lloyd (1944), Toner, Edwards & Curtis (1942), Grinnell & Palmer (1941) and Bray (1943). A well-marked peak appears in the ptarmigan curve in the years 1936–37 and 1937–38. There seem to be no accounts in the scientific literature about this apparent peak and following 'crash', but that there was indeed a notable increase during these two years is supported by a careful analysis of the replies to the questionnaires (see Table 1). This analysis showed the widespread nature of the rise, and made it clear that the great increase in the number of observers in the years 1935–36 and 1938–39 has not influenced the figures. The following comments from the Arctic Wildlife Enquiry returns for the year 1937–38 offer good supporting evidence for the increase:

> Thelon Game Sanctuary (Northwest Territories)....In western portion they are at a peak right now (Sept. 1937) or may even have passed it, but in eastern portion they are recovering from a fairly recent set-back. (C. H. D. Clarke.)
>
> From Fort Good Hope on Mackenzie River all the way down to Arctic Red River and to Aklavik, N.W.T....This last winter, 1937–38, ptarmigan were as thick down here as they have ever been. (J. E. Nagle.)
>
> Ptarmigan and Clinton Colden Lakes, District of Mackenzie....Unusually abundant...more numerous last fall than I have yet observed them in eight years. (A. J. Knox.)
>
> Lat. 59° North to 61° North, Long. 97° West to 102° West....Unusually abundant....More abundant by far than ever before in my 18 years of experience in the Sub-Arctic. (I. H. Smith.)

The year 1938–39 saw the return of ptarmigan numbers to an apparently lower level (there are no indications of any widespread scarcity) which was maintained—with the ruffed grouse numbers—until the next final year of abundance for North America as

a whole in 1941–42 (see Fig. 2 and Table 2). In addition to the literature references in Table 2 there are others which it has not been possible to incorporate therein that contain information on this phase of the cycle: Lloyd & Lanning (1948) and Speirs & Speirs (1947) record consequences of the crash in parts of Ontario, Rand's (1948) data suggests that the final year of abundance in the Cypress Hills of southern Alberta was either 1943 or 1944; and although Munro & Cowan (1944) found ruffed grouse scarce in south-eastern British Columbia in the summer of 1943, Rand (1944) found this species and spruce grouse common in the northern part of the province at the same time. Accounts covering a wide area occur in Cottam, Finley, Leopold & Cahalane (1943) who state 'This [1942] is the peak year of the ten-year grouse cycle from Alberta to the Lake States and even further...' and in Ferrie (nd. ? 1952) who gives graphs for Hungarian partridge (*Perdix perdix*), sharp-tailed grouse and blue grouse (*Dendragapus obscurus*) in the western provinces. These graphs fix the final year of abundance as 1942 in Manitoba and British Columbia and 1943 in Alberta and Saskatchewan. Among the replies to the Canadian Snowshoe Rabbit Enquiry questionnaires for the years 1940–41–42 there are thirteen that mention ruffed grouse or ptarmigan and only three of these report a decrease or scarcity. For the years 1942–43–44, on the other hand, twelve out of seventeen record diminishing numbers; and of the five reports of abundance or increase, three refer to the Yukon Territory in the year 1942–43.

The general crash reached its lowest ebb between 1944 and 1946; although in southern Labrador, in the Northwest River district, it seems from Grayce (1947)—and his remarks are borne out by the results obtained in the original grid-plotting—that there was a short-lived and local period of abundance of willow ptarmigan in 1944–45. By 1946–47 the tide throughout North America had begun to turn again (see, for example, Munro 1949) and the graph now shows a sharp rise until 1948–49. Here the annual ptarmigan records end—the graph points for the next two years being based on figures computed from the Hudson's Bay Company zoological reports for ruffed grouse only. Gabrielson & Wright (1951) found willow ptarmigan increasing in the Ungava district in the late summer of 1948 but state that rock ptarmigan and spruce grouse were scarce. Hildebrand (1950), who spent some time in much the same area that year, agrees on the abundance of willow ptarmigan but implies that rock ptarmigan were numerous in the spring. This discrepancy is perhaps explainable by invoking migration movements as its cause. Hildebrand found spruce grouse, too, at least locally abundant and quotes a report that the last year of abundance for this species occurred in the area about 1943. In Minnesota, Erickson, Highby & Carlson (1949) state that a recovery in the numbers of ruffed grouse was already noticeable in 1947, and Hale & Wendt (1950) remark that this species was flourishing in Wisconsin in 1949–50.

Discussing the pronounced drop shown in the graph after 1949–50, we find that from the literature there is the record of what was, perhaps, only a very local crash in northern Idaho in 1948–49 (Hungerford 1951); but by 1949–50 there is evidence that a more widespread decline was beginning in Canada. In that year the Hudson's Bay Company reports indicate that the main areas affected were north-eastern Alberta, north-western Saskatchewan and western Ontario. Cringan (1952) fixes the same date as the peak year for willow ptarmigan in the north-west of the last province, and Porsild (1951) remarks on the almost complete absence during the summer of 1949 of

rock ptarmigan in the Banks and Victoria Islands area of the Northwest Territories. In 1950–51 the few Snowshoe Rabbit Enquiry questionnaires that mention ruffed grouse suggest that the crash had extended to south-western Quebec, and the Hudson's Bay Company returns indicate decreasing populations in western Quebec, north-eastern Ontario, central Saskatchewan and central British Comumbia. However, official hunting figures indicate that ruffed grouse numbers had not yet begun to fall in Manitoba (Anon. 1952*b*), and Cowan (1952) and Rowan (1952) make it clear that over wide areas in the north of British Columbia and Alberta both ruffed grouse and ptarmigan were still exceptionally plentiful even until as late as 1951–52. But Rowan adds that he was informed that the 'prodigious numbers' of white-tailed ptarmigan to be found in 'the high altitudes of the Rockies north of Banff' in the winter of 1948–49 had an apparently unsuccessful breeding season in 1951 for 'very few young were seen during the summer'. That ptarmigan numbers were high in the Northwest Territories in 1950–51 and had been rising for the previous two years is suggested from the official hunting returns for that area (Anon. 1952*a*). Further east on Baffin Island, Wynne-Edwards (1952) reports that although rock ptarmigan were at a low ebb in the Clyde Inlet area in the summer of 1950 they were in above-average numbers at Navy Board Inlet at about the same time. By 1951–52 the area affected by the various crashes had extended to include southern Ontario, for Fowle (1952), discussing this part of the province, states: 'It appears to be the general opinion of the Field Staff of our Department that ruffed grouse have just passed [1951–52] the peak of abundance.' Dymond's (1952) remarks that: 'replies to the Royal Ontario Museum of Zoology questionnaires indicate that ruffed grouse populations increased in most parts of Ontario last year (1951)' apparently refer to a rather earlier period than Fowle's and possibly include a majority of replies from the more southern and heavily settled part of Ontario. Thus they are not necessarily at variance with any data so far presented. Finally, in the Thelon Game Sanctuary, Northwest Territories, ptarmigan appeared to be at or near peak numbers in the summer of 1952 (Tener *pers. comm.* 1952).

For the United States very little definite information on recent population changes is yet available for the last 2 years, but preliminary reports such as those published in the *Pittman-Robertson Quarterly* (**11**, 1951; **12**, 1952) and various State game bulletins suggest that tetraonid populations have reached high levels there and have already begun to decline in some areas.

To summarize: The main years of final abundance in the tetraonid cycle during the period under review have been 1932–33, 1941–42 and either 1950–51 or 1951–52, and most records of final years of abundance for large areas from whatever source fall within 1 year either way of these. That is, the mean cycle length is some 9 or 10 years. But this is a highly simplified account of a very complex phenomenon. For example, a point that emerges is that observers' opinions show much less unanimity about what is happening each year than is the case with the snowshoe rabbit; but, as has been suggested earlier, this may be because the amplitude of the tetraonid fluctuations is very much less than that of the small mammals and so changes cannot be so accurately assessed; or, on the other hand, it might be a real indication that synchrony between the various local cycles in tetraonids is actually not so marked as in the small mammals. At present it is not possible to decide. A glance at the curves in Fig. 2 will show how

seldom the excess of reports of either increase or decrease was higher than 50%; and this state of affairs is reflected in the reports for individual grid squares.

Furthermore, synchrony either between different major areas or between species, although normally very close, is seldom precise and there are a number of occasions when, even allowing for the relative crudities of the methods used in estimating peak abundance or final years of abundance, some areas show very marked deviations indeed from the general trend. For example: the individual reports of local crashes are mainly distributed over a 3-year period in that part of North America we have been considering; and in 1939 and 1945, according to the grid-plotting figures, the Northwest River district of southern Labrador experienced a combination of peak years that does not occur elsewhere. Edminster (1947) quotes some other examples. In the questionnaire results and in the literature other instances of a like nature can be found—occasional and isolated areas of abundance occurring at times of a general scarcity, and vice versa. The only example of notable asynchrony between *species* is that of the ptarmigan peak of 1936–37–38 which is not matched by any similar peak in the ruffed grouse cycle of that time. But in spite of these irregularities, that there is a very strong tendency for a general synchrony to exist among various tetraonid cycles over a great expanse of North America, is a fact that any theory put forward to explain the cause—or causes—of these cycles must take into account.

POPULATION FLUCTUATIONS BEFORE 1924–25

For this period we must rely on literature and the reviews made by others at an earlier date. Useful records go back for about 60 years, but these no doubt become less generally reliable as they extend further into the nineteenth century. From the following reviews and long-term records (Bump 1939; Clarke 1936; Comeau 1909; Criddle 1930; Darrow 1947; Edminster 1947; Fisher 1939; Forbush 1912; Lawton 1926; Leopold 1931; Leopold & Ball 1931; Rowan 1948; Schorger 1947; Snyder & Shortt 1936) which between them cover ruffed grouse, sharp-tailed grouse and willow ptarmigan, it is possible to fix those years in previous cycles, in or close to which most final years of abundance occurred throughout the greater part of North America; and it will be found that the majority fall within one year either way of the dates suggested, and that very few—if any—fall so wide of the mark as to be considered seriously out of phase. These years would seem to be (see Table 2): 1896, 1905, 1914 and 1923. Earlier dates still could be suggested but the evidence to support them as being generally applicable is too scanty. If one compares the dates given by the various authors just cited for the years of greatest general scarcity—which usually occur from 2 to 3 years after the final years of abundance—one finds an equally good agreement. Schorger's paper is of interest for his figures suggest that between 1857 and 1897 the crash in prairie chickens (*Tympanuchus cupido*) regularly preceded by a very short time that in ruffed grouse, and so 'high' years for the one were regularly 'low' years for the other. Leopold, in his graphs for the same area, does not however show any such reciprocal regularity.

There are numerous references to widely scattered areas of North America that supply further evidence of the widespread nature of the tendency towards synchrony of the tetraonid cycle in these earlier years. As many of these have not been quoted

previously in such a context as this it may be worth while to give them at some length:

For Ontario all the following report either directly or indirectly on the 1923 final year of abundance for grouse in that province: Bensley (1928), Fargo & van Tyne (1927), Macnamara (1925), Magee (1922, 1923), Mitchell (1929), Snyder (1935, 1938), Snyder *et al.* (1928) and Snyder & Baillie (1923). For Alberta, Rand (1948) remarks that Young found ruffed grouse common in the Waterton Lakes Park in 1922 and Lawton (1926) states that sharp-tails were becoming scarce in the Province in 1924. In Saskatchewan, Bradshaw (1924–26) records a falling-off in ruffed grouse in 1923–24 and in sharp-tails in 1925–26; and for British Columbia the period of abundance before the crash of 1923–24 is commented upon in various ways by Kelso (1926), Munro (1930), and Swarth (1924). Snyder (1935) gives an earlier date for an abundance of sharp-tailed grouse in this province as having occurred in 1911. For the Northwest Territories reports on the status of ptarmigan and various species of grouse may be found in Blanchet (1925), Rowan (1925), and Williams (1922, 1933): apparently all species were in good numbers in the Mackenzie District between 1921 and 1924, but by 1925—according to Rowan—ruffed grouse had become scarce south of the Great Slave Lake. In the United States, it appears from Schwartz (1945) that 1923 was the final year of abundance for the prairie chicken in Missouri.

For the years of dearth after the peak years of about 1914–15 and the increase in numbers leading up to the next crash, see Taverner (1929) who reports on aspects of the phenomenon for various parts of western Canada.

NEWFOUNDLAND AND THE MARITIME PROVINCES

These are taken to include New Brunswick, Nova Scotia and Prince Edward Island. Although the questionnaire data for this part of Canada stem from a source quite distinct from that for the remainder of the country (the Biological Board of Canada Reports 1932–33 to 1939–40), it was not originally expected that it would be necessary to treat this information separately. However, it soon became clear that in this area the grouse fluctuations were distinctly out of step with the rest of Canada and the northern and eastern states of the U.S.A. Furthermore, on consulting the literature, mainly confirmatory evidence was found, and it now appears that for about the last 20 years at least the Maritime Provinces have *consistently* experienced their crashes about three years ahead of the remainder of the ruffed grouse range as a whole, even before the nearby states of Maine, Vermont, New Hampshire, Massachusetts and Connecticut—for the New England fluctuations see Bump (1939), Darrow (1947), Frank (1946), and Gross (1931, 1932). The evidence upon which these statements is based is as follows:

Lloyd (1921) states that ruffed grouse were abundant in New Brunswick in October 1919, and Townsend (1922) and Tufts (1925, 1952) remark that they were numerous in Nova Scotia in 1921 and 1922. Tufts (1925) and Darrow (1947) fix 1923 as the final year of abundance for Nova Scotia and New Brunswick and a scarcity seems to have followed until about 1927, when Rand's note (1930) that ruffed and spruce grouse were common at Fishers Lake, Annapolis Royal, N.S., in the summers of 1927 and 1928, indicates that recovery was taking place. Nevertheless, the hunting season

remained closed in Nova Scotia until 1930, although according to Clarke (1936) the next peak year and final year of abundance occurred in this province in 1928–29, followed by a decline beginning in 1930 and lasting until at least 1932. On the other hand, Darrow (1947) gives 1930 as the final year of abundance for Nova Scotia. The Biological Board of Canada's annual reports for the Maritime Provinces begin in 1932 and continue until 1940 but do not include Newfoundland (where ptarmigan occur but not ruffed grouse). The replies to the questionnaires are in sufficient numbers to be considered reliable (see Table 1) and generally corroborate the statements made by the previous authors in suggesting a final year of abundance before 1932 (in about 1930 according to the majority of opinions expressed on the date of the last remembered year of abundance), followed by a decline ending in 1933–34 and another probable peak in 1938–39. Clarke's statement that a peak occurred in New Brunswick in 1931 is in fairly good agreement with this, but not Darrow's of one in 1933. On the 1938–39 abundance Tufts supplies the following interesting data:

Year	1938	1939	1940	1941	1942
Number of ruffed grouse flushed per hour	2·40	2·27	1·09	0·90	Rather scarce; no record kept

The annual reports of the Nova Scotia Department of Lands and Forests (Anon. 1938–) overlap slightly with those of the Biological Board of Canada and agree with them in indicating a peak about 1938–39; but Williams (1952) gives the following record of the ruffed grouse kill in New Brunswick during the open seasons of 1940–41–42 as: 35,065, 45,245 and 61,280 respectively, which suggest a later peak in that province at least—and this is borne out by Darrow's date of 1942 as the final year of good numbers there. The most recent reports of the Nova Scotia Department of Lands and Forests suggest that the last final year of abundance for the province as a whole occurred in 1948; and an analysis of the replies to the Snowshoe Rabbit and Ruffed Grouse Enquiry of 1951–52 for the Maritime Provinces does not indicate a high tetraonid population during that year, the previous final year of general abundance being stated by most to have been about 1949.

For Newfoundland there is very little information available. Clarke gives the peak year for ptarmigan as 1927 or 1928 depending on the district, with declines in 1928 or 1929 and a minimum in 1932.

Summing up then: the majority of the individual reports suggests that the main final years of abundance for the Maritime Provinces as a whole (with the possible exception of Newfoundland of which so little is known) have occurred about the years of 1922, 1930, 1939 and 1949. In addition, there is one report of unusual abundance of ruffed grouse on Prince Edward Island in 1912 given by C. R. Palmer in his 1934–35 report to the Biological Board of Canada, and another from the same source by W. G. Harris of abundance in at least part of Nova Scotia—approximately between the years 1898 and 1905. But in view of the considerable measure of disagreement that does exist on the dating of the cycle and because of the importance of establishing beyond doubt that the Maritime Provinces have (or have not) a cycle of their own, the whole question of game-bird fluctuations in this part of Canada is obviously in need of very careful study in the future.

ALASKA

Useful records for Alaska begin with the present century: Buckley (1952) remarks that the year 1906 was a year of abundance for ptarmigan on the Seward Peninsula in western Alaska, and Leffingwell (1919), giving an account for the north-east that covers the period from 1907 to 1914, states: 'In 1907 on Okpilak River not more than a couple of dozen were obtained with a shot gun. In 1908 perhaps fifty were shot on the Canning. During May and June of 1912...twenty-five were obtained in a single day's march. About 250 were secured in all before the ammunition gave out. In 1914 the Canadian Expedition at Collinson Point consumed about twenty birds daily for 2 or 3 months. Most of these ptarmigan were secured within 15 miles of their camp.' On the face of it, this account seems to describe a typical recovery from a 'low' of about 1907; and Williams's report (1925) of good numbers of rock ptarmigan on the Yukon-Alaska boundary in 1911 is in conformity with it. Buckley (1952) continues the story: 'In 1913...ptarmigan were very abundant along the lower Kuskokwim...and were reported extremely abundant in 1915 along the Alaska Range and in the vicinity of Fairbanks and the entire Tanana Valley.' That a crash occurred some time between 1915 and 1919 is implied by Bailey's statement (1926) that 'in 1919 ptarmigan were very scarce throughout the territory...in 1920 the birds began to return and in 1921 they were reported abundant at all points where they usually occur'. This waxing of the population continued, for in the Annual Report of the Governor of Alaska (Bone 1923) it is stated (p. 51) that game birds were increasing at this time and that grouse and ptarmigan were plentiful. According to Clarke (1936) ruffed grouse had a peak in 1922–23 with a decline in 1924 and a minimum in 1927 but his information was scanty, and perhaps of only local significance. Brandt (1943) comments upon the good numbers of willow ptarmigan in the spring of 1924, adding on the subject of the Yukon ruffed grouse that, 'this was evidently then at the bottom of the cycle...in northern Alaska'. Buckley, on the other hand, remarks that in 1923 and 1924 ptarmigan were abundant along the Savage River and near Wild Lake, and that in 1925 *all* tetraonids were abundant in the interior of Alaska. That this period was one of general abundance for ptarmigan at least, is suggested by Conover's statement (1926) that willow ptarmigan were very plentiful in the Kuskokwin Mountains in the summer of 1924 and common at Point Dall at the same time. Bent (1932) quotes Warburton to the effect that 'the scarcity of these birds [willow ptarmigan at the mouth of the Yukon River in the summer of 1929] was a great disappointment. I had expected to find them as plentiful as...about Nome and Teller, Alaska, in the summers of 1924 and 1925. At that time on the Seward Peninsula they were most plentiful, together with many rock ptarmigan'; and Laing (1925) found rock ptarmigan very numerous in the Aleutian islands of Adak and Atka in the spring of 1924. Apparently 1926 was the final year of abundance for most of the Territory, but according to Buckley ptarmigan remained plentiful until 1927 in the area south of the Alaska Range. After this there was general scarcity until the early 'thirties when Buckley (1952), Clarke (1936) and Snyder (1935) all comment on the increase in numbers of the various species. Clarke reports a final year of abundance for ruffed grouse in 1933, but he is alone in this—Buckley states that both species of ptarmigan and the three species of grouse reached

their peak by 1935 or 1936 over most of the Territory, with some areas having their peaks delayed until as late as 1938. Once more there follows a period of scarcity, with good numbers occurring again in various districts between 1942 and 1946. Rausch reports (1951) that in the Brooks Range area during 1945 'a heavy mortality in willow ptarmigan' was observed.

A valuable account by a single observer that covers much of the period we have been discussing is given by Murie (1946) for the birds of the Mount McKinley National Park. The substance of this is as follows: in 1922 and 1923 willow ptarmigan were very plentiful and continued so until 1926 when their numbers were probably even greater. After 1926 they became scarce but reached another peak in 1933. They were very abundant from 1933 to 1936, but scarce in 1938. From 1939 to 1941 they were common but far from the abundance observed in 1923. They were on the increase and in 1943 were reported very plentiful, so apparently were nearing another peak in the cycle. In 1945 they appeared to be only slightly more plentiful than in 1941. This account from a relatively small area of Alaska is in excellent agreement with the general picture we have obtained for the rest of the Territory.

At the present time tetraonids are once again on the increase (Gruening 1951, p. 63; Buckley 1952) and there is no sign yet that a general peak of abundance has been reached. In the Snowshoe Rabbit Enquiry reports for Alaska for the year 1951–52 there are twelve replies to the section on 'grouse'. Of these seven record increasing or abundant populations of the various species of tetraonids, three record normal numbers or no change over the previous year, and only two state that there has been a decrease or scarcity.

All the evidence we have reviewed (with the sole exception of that of Clarke) is in satisfactory agreement with the hypothesis that the tetraonid cycle in Alaska is an approximately 10-year one with final years of local abundance being most general just after the middle years of each decade. Synchrony between the various species in any one area seems to be fairly well established (although Brandt cites what appears to be an obvious exception) and this is remarked upon by Buckley and implied by Dufresne (1942). As we have seen to be the case with the tetraonid fluctuations in other parts of North America, synchrony between different areas is close rather than precise, and on this point Buckley makes the comment: 'There is some evidence of a difference in time in peak populations, with the peaks being reached first in the north and west, with a lapse of up to two years for peak populations south of the Alaska Range. The same situation prevails on the Alaska Peninsula with periods of abundance preceding those in the Anchorage area.'

A well-marked cycle in the numbers of tetraonid game birds occurs throughout most of the northern part of North America. Although in any one restricted district the length of the cycle may vary within fairly wide limits, there is a strong tendency over enormous areas for crashes to occur in synchrony every 9–10 years. In most of Canada and in the northern United States one main cycle appears to operate (or at least the methods at present used to study the phenomenon do not demonstrate within this great area the occurrence of any consistent differences). However, in the east, in the Maritime Provinces of Canada the cycle seems to be advanced in its corresponding stages by about 3 years over the 'main' cycle; whereas, in the extreme

north-west in Alaska, the cycle appears to be retarded by about the same interval. Not only does a similar phenomenon appear in the snowshoe rabbit cycles (see Chitty 1948, 1950*a*—the 1948 paper for a list of earlier publications on snowshoe rabbit fluctuations), but wherever tetraonid game birds and snowshoe rabbits occur together the population fluctuations of each—when large areas are considered—also take place in close synchrony.

GREENLAND

According to Salomonsen (1951) three races of *Lagopus mutus*, the rock ptarmigan, occur in Greenland. There are no other gallinaceous birds. Apart from Manniche's (1910) statement that ptarmigan were common in the north-east in the vicinity of Germania Land in 1907–8 and Pedersen's (1942) report that they were distinctly scarce in much the same area in 1938–39 but commoner further north, the more reliable records have been summarized by Salomonsen as follows: 'Particularly significant peak years were in 1890–91 in S. Greenland (Helms, Møller), 1929–30 in N.E. Greenland (Schaanning) and 1948–49 in the whole of Greenland.' Schaanning's evidence (1933) for a peak in 1929–30 seems well supported by his hunting figures. More recently, Salomonsen (1952) added these comments: 'As to the last peak (in 1948–49) I can say a little: Ptarmigan were common in 1948, still more common in 1949 (when I was in Greenland), and to my surprise I got the information that it was common in 1950 also. In 1951, however, there were only very few....In 1946 ptarmigan were very scarce.'

Braestrup (1941) gives an almost continuous record between the years 1882 and 1939, and it is upon this record that the 3- to 4-year cycles claimed by Lack (1951), Palmgren (1949) and Siivonen (1948) have been based. Such an interpretation is possible however only if all the minor fluctuations shown in Braestrup's graph (p. 74) are taken into consideration. Braestrup himself thinks that his data indicates an approximate 10-year periodicity—for arctic hares as well as ptarmigan—with peaks (according to my reading of his graph) in North Greenland in 1892, (?) 1897, 1914, 1927 and 1938; and in South Greenland in 1894, 1904, 1918, 1927 and 1937. Discrepancies with Salomonsen's 'significant peak years' are evident.

Whether there is any measure of agreement between the North American and Greenland cycles yet remains to be proved. The evidence at present available for the dating of the Greenland fluctuations is insufficient for the drawing up of any reliable series of peak years or final years of abundance which could be used for a comparison, and there is therefore a great need for a careful study of ptarmigan fluctuations in Greenland to be undertaken in the future.

ICELAND

Although the rhythmical rise and fall of ptarmigan numbers in Iceland was commented upon as long as 30 years ago by Kloster (1923) and a few years later by Hachisuka (1927), the most valuable account that has so far been published is the recent survey made by Guðmundsson (1951) of the population changes there in the sole local race, *L. m. islandorum*. The main source of data for this survey was the Icelandic trade record which includes among its statistics the figures for the annual export of ptarmigan. Normally—as Guðmundsson readily admits—the use of export figures in an

investigation such as this has serious disadvantages which make it necessary to treat any conclusions reached with caution. For example, no account is generally taken of home consumption, which may be considerable, the whole of a season's kill may not be exported in the same year. However, in this particular case, Guðmundsson (1952) states that until recently ptarmigan was not a popular food in Iceland and the good price fetched by the birds led to a very high proportion of the total kill being exported. Furthermore, about 90 % of the birds taken each season are exported in the same year since they are not frozen beforehand and so must be got rid of promptly. Therefore, Guðmundsson maintains, the use of these particular export figures is not subject to the usual objections, and in this view he would seem to be justified. For more recent years he supplements the trade figures with field observations made by himself and

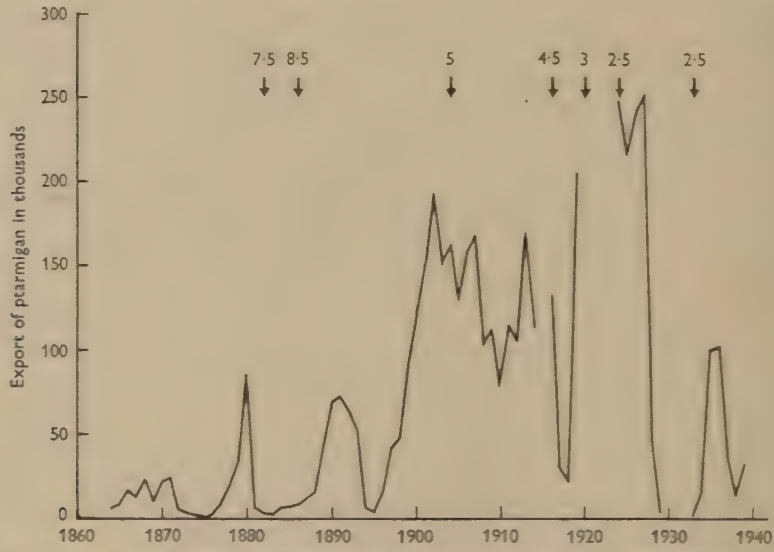

Fig. 3. Exports of Icelandic rock ptarmigan (from Guðmundsson 1951). For explanation see text.

others. The conclusion reached by Guðmundsson is that ptarmigan exhibit an approximate 10-year cycle in Iceland, regular from the time records begin in 1864 until about the beginning of this century, then rather irregular until about 1927 and finally, regular again until the present day. In his paper Gudmundsson does not actually state the dates of the peak years or final years of abundance indicated by his data: therefore I have prepared a graph from his table and this is given in Fig. 3. Some comment is needed: first, it will be noticed that the records from some years are missing. With the exception of 1920 these are years in which ptarmigan were completely protected. Years marked by arrows are those in which the length of the open season was altered: up to and including 1881 there was an open season all the year round, thereafter the length of the open season until the next alteration occurs is given in months over the arrow. It does not appear permissible to make proportional corrections to the yearly export figures in an attempt to compensate for these changes;

neither does it appear likely that any of these changes could materially affect the conclusions to be drawn from the curve—except for the one occurring in 1904 when the season was shortened by 40%, from 8·5 to 5 months. Here the magnitude of the change is so great and the difference between the export figures immediately before and after so relatively small, that the occurrence of a clear peak in 1902 may well be doubted.

Reading, then, from the graph the general peak years or final years of abundance appear to be 1871, 1880 (see Clarke & Backhouse 1885, for a report of the crash of 1880–81), 1891, (?) 1902, (?) 1907, 1913, 1927 and 1936. It does not seem likely that any of the missing years have been general peak years or final years of abundance; Roberts (1934) referring to 1932 states: 'Not a single specimen was seen on the coast.' Gudmundsson (1951) brings the record up to date from 1939 with the following information: there was a great abundance of ptarmigan from 1943 to 1945 inclusive, but in 1946 the ptarmigan population underwent an extensive and sudden decline, reaching its lowest ebb in 1947 and 1948. (See also Yeates & Jeans 1949.) At present (1952) the cycle is on the upgrade and is expected to reach its peak about 1953.

Here we have a rather irregular cycle almost certainly out of step with that in nearby Greenland, out of step with those in North America (although there is some resemblance to the Alaskan) and, as will be seen presently, of a different frequency from that found in Britain.

BRITISH ISLES

A very recent appraisal of tetraonid fluctuations in this area has been made by Mackenzie (1952), and it is upon this, which incorporates data in an earlier paper by Middleton (1934), that the discussion in this section will mainly depend. According to Moran (1952) and Mackenzie there is a fair degree of synchrony in the British Isles between the fluctuations of red grouse, ptarmigan and capercaillie (*Tetrao urogallus*) populations and, to a lesser extent, those of black grouse (*Lyrurus tetrix*). Taking the red grouse cycle as the standard of comparison since it is by far the commonest and best documented species, Mackenzie shows that 73% of the peaks of the other species fall within one year either way of the red grouse peaks, and Moran demonstrates the relationships of the various cycles to each other by statistical methods. The mean length of the combined tetraonid cycle is about 5 or 6 years—depending on the period being studied—and from Mackenzie's text-figures nos. 2 and 3 it is possible to draw up a list of general peak years starting from 1860. These are: 1862, 1866, 1872, 1876, 1881, 1888, 1896, 1901, 1906, 1912, 1915, 1922, 1927, 1930, 1934, 1938, 1941 (see Fig. 6). This gives a cycle length for this particular period of 5 years and a very high proportion of the individual peak dates cited for the various species fall within one year of these. (It is perhaps worth noting, without attaching undue significance to it at present, that 74% of the peak dates given by Middleton for the partridge—*Perdix perdix*—either coincide with, or fall within one year of, many of those in this series also.)

Examining the data for one species—the red grouse—in greater detail, we find that when the fluctuations of any *individual* moor are compared with those of the main series there is a marked degree of asynchrony apparent. Instead of the fairly regular approximately-five-year cycle characteristic of the larger area, we find that intervals

between peaks vary, the range being from 3 to 10 years. This fact prompted the drawing up of a diagram to show the percentage of red grouse moors reaching a peak each year, and the result is shown in Fig. 4. Although there is excellent agreement between the main peak years found in this way and those found by Mackenzie by plotting total kills, this graph allows us to draw conclusions that were not quite so evident in Mackenzie's method of presentation. Not only is great regularity apparent in the cycle up to 1912; but we see that, in spite of the strong tendency toward synchrony, in the 80 years between 1860 and 1940 only on four occasions did more than 50 % of the moors in any one year experience a peak together—the range throughout varying from 0 to 64 %. The very local nature of the occurrence of peaks even in the best of years is thus immediately apparent. After about 1913 a notable change occurs in the rhythm of the cycle—probably because of the first World War and its effects through social and other changes on the management of the moors, and it is evident from the graph that the change in the general rhythm beginning then has continued until the present day.

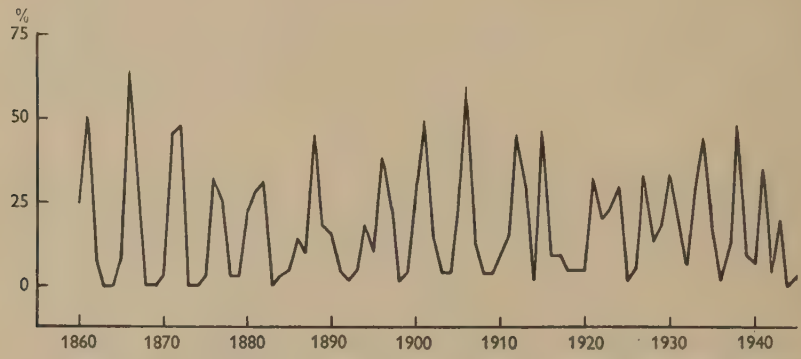

Fig. 4. Percentage of British red grouse moors reporting peak populations (from Mackenzie 1952).

NORTH-WESTERN EUROPE

For Norway the work of Kloster (1921, 1922) on *Lagopus lagopus* has long been accepted as the standard account and has been used as such by later authors such as Brinkmann (1927), Johnsen (1929) Nordhagen (1928) and Siivonen (1948) in their respective attempts to explain the phenomenon of population fluctuations in this part of Europe. Kloster himself admitted that not only was his source of records very limited but that the records themselves left much to be desired. However, a recent review and re-presentation of his work by Hagen (1952), together with some new data from 1916 onwards, has done a great deal to establish confidence in Kloster's original postulate of an approximately 4-year general cycle. Siivonen (1948, 1952) has suggested a 3- to 4-year cycle—more particularly one averaging $3\frac{1}{3}$ years—to apply to tetraonid populations in Scandinavia, Finland and beyond; and although much of the evidence presented in his earlier paper was unsatisfactory because of the smallness of the number of birds involved in his graphs and tables, Siivonen has now marshalled more convincing information in support of his hypothesis—but only in so far as the

Finnish fluctuations are concerned. This new information is garnered mainly from hunting season statistics extending back to 1906 and from quantitative data on breeding success in capercaillie, black grouse and hazel grouse (*Tetrastes bonasia*) throughout the country during the period 1946–52 inclusive. For this latter period Siivonen states that in all three species significant differences exist between the mean peak and non-peak year figures found for clutch-size and for brood-size (after 1 July), and that in capercaillie and black grouse significant differences occur between the mean numbers of unhatched eggs found in the nests in peak and non-peak years. (The peak years are those as defined by the various hunting season statistics.) Some of the black grouse clutch-size figures cited for 1952 do not seem to be in accord with Siivonen's generalization and these apparent exceptions are not explained. Discussing Siivonen's earlier paper, Kalela (1951) suggests, as did Palmgren (1949), 'that Siivonen's $3\frac{1}{3}$ year periodicity is to a great extent. . .identical with more or less typical random variation of cycle length'. But whether this is indeed true of the phenomenon as a whole still remains to be proved. (Cole (1951) should be consulted for a more general review on the resemblances between random fluctuations and some population cycles, but it should be kept in mind that he has not included the most regular cycles in this discussion.)

Probably as reliable a source of information as any discussed in this section (and one which reinforces the case in favour of a short cycle) is Ruden's series of papers (1927–40) on the status of the wildlife populations in various districts of Norway. Reports from between 30 and 40 of these districts were received each year and degrees of abundance were indicated according to the following scale: 'none', 'poor', 'average', 'good', 'abundant'. I have taken the replies on willow ptarmigan (those for capercaillie and black grouse yield very similar results on analysis) and have treated them in the same manner as has already been used in dealing with the various Canadian questionnaires—in this instance combining 'abundant' with 'good' and 'poor' with 'none' and graphing the excess percentage of the one combination over the other. The result, shown in Fig. 5, indicates general peaks in 1930 and 1934 with the possibility of another about 1926. Although the main years of overall abundance are clearly marked, it is evident from my percentage figures how few areas, even in general peak years, were recording populations higher than the average. In fact, the proportion rises only once above one-third of the total—indicating a low degree of synchrony. Siivonen (1948) has divided Ruden's results into those for north, central and south Norway. The differences that now appear between each area are not great and do not seem to me to be significant. However, Siivonen suggests that they show that the general peaks tend to occur later with increasing latitude—a conclusion rather at variance with the findings for Finnish tetraonids given in his 1952 paper, where synchrony is shown to be very close between the various species throughout the whole country, although the intensity of the fluctuations is claimed to become more marked at higher latitudes.

In Denmark a short-term study of a tetraonid fluctuation has been made by Westerskov (1943). It concerns the black grouse and covers the years from 1927 to 1941 inclusive. I have taken the data embodied in his figs. 34–37 (official reports on abundance ranging in number from 80 to 150 each year) and have treated the replies in the

same way as has already been done with the Canadian questionnaires and Ruden's Norwegian series. The resultant graph (Fig. 5) shows a clear final year of abundance in 1934 with 'spikes' in 1929 and 1938. Westerskov's own graph for those replies recording *only* abundance greater than normal (fig. 34, p. 65) also shows a clear peak for 1934. For Sweden, Hamilton (1944) fixes 1942 as the peak year within the period 1939–44.

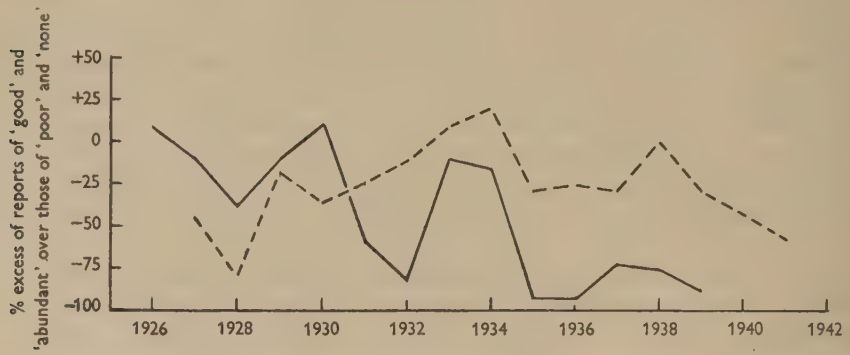

Fig. 5. Fluctuations in Scandinavian tetraonid populations. ——, Norwegian willow ptarmigan (from Ruden 1927–40); – – –, Danish black grouse (from Westerskov 1943).

If we now compare all the above series for the period in which they overlap, we obtain the following scheme of most general peak years (a few extremely doubtful peaks have been excluded):

Hagen and Kloster	1911–12	1914	—	1921	1923	1926	1930	1934	1938	—
Hamilton	—	—	—	—	—	—	—	—	—	1942
Ruden	—	—	—	—	—	—	1930	1934	—	—
Siivonen	1911	1914	1918	1920–21	1923–24	1926–27	1930	1933–34	1937	1942
Westerskov	—	—	—	—	—	—	—	1934	?1938	—

A great deal of agreement is obvious and this would be increased even more if all the most doubtful peaks were included. If we accept Hagen's and Kloster's series up to 1911 and Siivonen's from 1942 to date, and fuse the various series in their period of overlap (which seems a permissible step in view of the amount of agreement apparent) we obtain the following combination of peak years to support the hypothesis that a short cycle obtains in north-west Europe: 1872, 1875–76, 1880, 1883, 1887, 1891, 1894–95, 1897–98, 1903, 1906, 1909, 1911–12, 1914, 1918, 1920–21, 1923–24, 1926–27, 1930, 1933–34, 1937–38, 1942, 1944–45, 1948, 1951 (see Fig. 6), that is, an average cycle length of about 3·4 years; and it will be seen from Elton (1942) and Wildhagen (1952) that this series is almost identical with that for the Norwegian 'lemming years'. Furthermore, it also accords well with the peak years given by Johnsen (1929) in his eagle bounty curve.

Evidence claimed to support the theory that at least the Finnish cycle has an approximately 10-year periodicity has been presented by Airaksinen (1946). The evidence in this case consists of the annual export figures of the various game birds—capercaillie, black grouse, hazel grouse and willow ptarmigan—taken together from the year 1867

onwards. Final years of abundance according to my reading of Airaksinen's graph occurred in 1868, 1887, 1896, 1906, 1913 and 1923, and the resemblance of this series to the main North American is obvious. However, there are objections to be met; the first of which is (as has already been indicated in the section on Iceland) that although export figures give a continuous and good numerical record, there is no guarantee that they accurately mirror either the total kill each year or the actual status of the populations themselves. Secondly, when a series is made up of figures referring to a number of species, the series is reliable only to the extent that the species fluctuate in unison. This Siivonen (1952) seems to have established for the various tetraonids in Finland.

Other studies of the northern Scandinavian problem, such as those by Dahl (1936), Olstad (1948) and Holt (1950), help but little in resolving its difficulties—either the figures given are too low for reliability, the period covered is too short or the area dealt with is so small that only the irregular local variation is apparent.

SOVIET RUSSIA

There is, unfortunately, very little information available on game-bird fluctuations in the U.S.S.R.; and those few papers that I have been able to consult do not permit of any definite conclusions being drawn as to the nature of the periodicity.

Formozov (1935) treats with population fluctuations in various species of game birds in widely scattered places; but the only data that describe in any detail what might be called a long-term variation in numbers in a particular area, refer to the north-western extremity of the country. Formozov states that in East Murman 'there was a mass appearance of willow grouse' in the winter of 1918–19 and goes on to say that 'around Murmansk their numbers have varied as follows of recent years:

> 1924—Year of abundance. [Willow] grouse in mass numbers.
> 1925—None at all.
> 1926–29—Few.
> 1930—They begin to be found in large numbers.'

He quotes another Russian author to the effect that in the Archangel Government there was an abundance of feathered game in 1912 and 1913 followed by a crash in 1914 and a scarcity that continued until 1916 with the beginning of a recovery in 1917. We are not told whether the effect of the first World War has been taken into account here. Semenow-Tian-Shansky (1939) remarks of *Lagopus mutus* in the nearby Lapland Reserve on the Kola Peninsula: '1930 was a year of abundant output, whereas the summer of 1931 was very unproductive of ptarmigan. . . . After that the percentage of young birds increased every year and the ptarmigan population increased at the same time until the winter of 1934–35 which was catastrophic.' Severtzoff's (1934) paper on the population dynamics of vertebrates might usefully be quoted here, for it contains a section dealing with partridge fluctuations over 25 years in the imperial hunting estate of Gatchino near what is now Leningrad. From graphs and tables it appears that peak populations occurred for this species in the years 1891, 1898, 1901 and 1906—the record extending from 1886 to 1909. Capercaillie on the same estate did not show any clearly cyclic population changes during this period.

If it were assumed that these various populations were exhibiting a degree of synchrony throughout the whole of the period under review similar to that known to occur over comparable areas in North America, then together they would form a series with general peaks in 1891, 1898, 1901, 1906, 1912–13, 1919, 1924, 1930 and 1934—that is, with a periodicity of about 5 years (see Fig. 6). However, we have no way of being sure that such an assumption is justified.

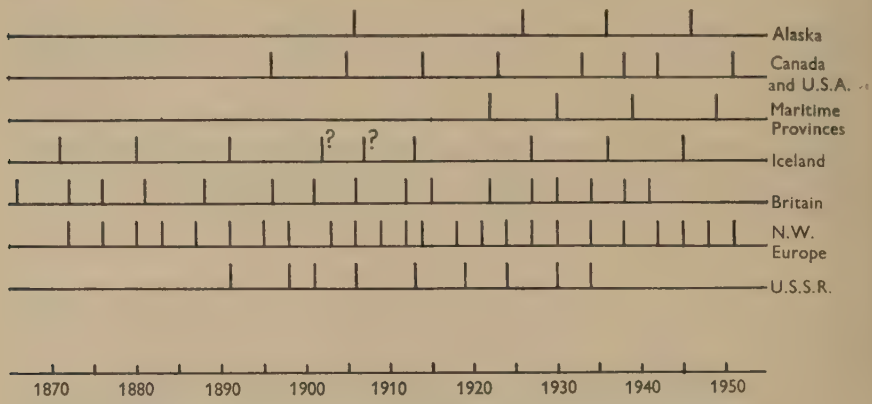

Fig. 6. Main peak years or final years of abundance for various northern hemisphere tetraonid populations.

SPITSBERGEN

Although casual references to the numbers of Spitsbergen ptarmigan (*L. m. hyperboreus*) for as far back as the middle of the nineteenth century can be found in the literature, it is extremely difficult to obtain anything like a continuous record for the fluctuations that are stated by Johnsen (1933) to occur there. A review of early authors is given by le Roi (1911) in the course of a more general discussion, but the most reliable starting period for our present purpose would seem to be that between the years 1909–11 when three independent authors recorded good numbers (Mathey-Dupraz 1911, 1913; Munsterhjelm 1911; Lövenskiold 1952). Other years of abundance appear to be 1913–14—when two men trapped more than a thousand birds in one very restricted area during that season (Lövenskiold 1952)—and 1918–20 (van Oord 1921; Jourdain 1922). An overall scarcity lasting from about 1921 to 1924 is then indicated by the remarks of Gordon (1922), Jourdain (1922), Longstaff (1924), and Montague (1926); and this is followed by a period of abundance between the years 1925 and 1929 according to the trappers' diaries quoted by Lövenskiold. Although Dalgety, McNeile & Ingram (1931) state that ptarmigan were reported plentiful in the winter of 1929–30, the entries in the trappers' diaries for the same period are in agreement that the population was at a low ebb at this time—possibly because different areas were being reported on. From then until the 1935–36 season the information given by Lövenskiold is such that it is not possible to decide whether a definite peak or period of abundance had occurred, but there seems to be little doubt that ptarmigan were again in general good numbers throughout the winters of 1936 and

1937. A crash is then indicated for the 1937–38 season, and Lövenskiold's records come to an end in 1940, by which time there are signs that numbers as a whole were once more returning to a high level.

The Spitsbergen information—although by no means as full as we would wish—is at least sufficient, I think, to establish that the cycle in this area is a short one; but as our data do not permit us to fix—except very approximately—the final years of abundance for each period, the question as to whether this cycle is, or is not, connected with any in north-western Europe must await further investigation.

DISCUSSION

We have shown that throughout those parts of the Northern Hemisphere for which we have data, populations of various species of tetraonid game birds experience periods of abundance in common over wide areas and that these periods are terminated by well marked declines in numbers ('crashes') that tend to occur in synchrony.

When we come to examine some of these large areas in more detail we find that the cyclic population changes in each species as a whole are made up of many local cycles of rather irregular periodicity which generally include a spell of about 2–3 years when most observers report abundance—apparently at those times when numbers are approaching a peak, are at a peak or are just beginning to decline. The crash in each local cycle is normally fairly sudden and is generally most marked in its first year, although numbers usually continue to diminish for at least another year before becoming stationary or beginning to increase once more. Mackenzie (1952) has shown this pattern to apply to British tetraonids (where the periodicities of the local cycles vary from 3 to 10 years), and among tetraonid game birds in North America the data from individual reporting stations are in conformity with it.

Although there may be disagreements between the periodicities of the local cycles, there is a general tendency towards synchrony such that in North America individual peaks or final years of abundance show a greater degree of coincidence every 9–10 years than at other times, in Britain this interval between successive maximum coincidences is about 5 years and in north-west Europe every 3–4 years. Final years of dearth show the same tendency, but in both cases the degree of coincidence is not great—seldom exceeding 50 % in any one year in most major areas. It must be remembered that those localities not reporting peaks or final years of abundance are not necessarily recording minimum populations. There is a distribution of population densities among the remainder of the reporting stations varying from great scarcity to near abundance. For instance, some of these local populations are still increasing, some diminishing and some remaining stationary. The proportion of individual localities reporting peaks or final years of abundance within one year either way of the main regional maxima has been shown in some cases to be about 75 % (Mackenzie 1952).

If there is this rhythmic tendency to synchrony every 10 years or less and there is a period of 2–3 years in most local cycles when numbers are likely to be considered high by most observers, then we should expect to find at least 1 year in each major cycle when there will be almost unanimous agreement that a state of universal abundance exists. However, we have seen that this does not mean that the degree of coincidence between the actual *peaks* or *final years of abundance* needs necessarily be

high at this time. Furthermore, as the true mean periodicity of a major cycle depends upon the distribution of periodicities among its constituent individual minor cycles (measured from each true peak or final year of abundance to the next), we should expect that as this distribution alters so, too, should the interval alter between each successive period of universal abundance—and this, in fact, is what is actually found to be the case: in the so-called '9·6 year' cycle the intervals between the general peaks vary mainly between 9 and 10 years, and in the '$3\frac{1}{3}$ year' cycle the general peak intervals normally vary between 3 and 5 years, and so on.

Any theory offered to explain fluctuations in the populations of Northern Hemisphere animals has not only to account for the fact that so many classes of animals are affected —fish, mammals and birds (Dymond 1947, Elton & Nicholson 1942)—and that there is this tendency to widespread synchrony; but also for the fact that although the small rodent cycle has the same or a very similar periodicity (of about 4 years) in both north-western Europe and arctic Canada, the tetraonid cycle is apparently synchronous with it in one case but not in the other. That we have been able to demonstrate the existence of two major tetraonid cycles would seem to dispose finally of the theory (advocated, among others, by Rowan 1950) that there is a direct extra-terrestrial cause since we should expect so powerful an influence to exert a similar effect throughout; and, besides, we should also expect to find not only a greater degree of synchrony within any one major area but also no consistent time lag such as appears to exist between the three main North American regions. (It may well be that the method used in the present investigation for dealing with the North American data has suggested a degree of *discontinuity* between these three regions that does not actually exist; but that there is a *difference* in the dating of the general cycles between the extremes of Alaska and the Maritime Provinces seems certain, and this conclusion is supported by the results already cited for the snowshoe rabbit.)

Siivonen's theory (1948) of the co-existence of short and long general cycles whose periodicities are in a particular simple proportion to each other now also appears untenable—the present data give no indication that the periodicity of the North American cycle is an exact multiple of that of the European. Lack's suggestion (1951) that predators may serve as the synchronizing agents between what he considers the primary mammalian and the secondary avian cycle would seem to require too complicated a system to account for so widespread a phenomenon involving so many species; and besides, there are certain clear instances when the birds are known to have preceded the mammals locally in a crash (see Clarke 1936; Greene, Evans & Larson 1943; and Rowan, this paper, p. 9).

Although the temptation to join with so many others in speculating about causes is great, to do so at length is probably fruitless until we have more data. However, it does seem that weather systems must play an important part. But, so far, all attempts to find a climatic factor correlated with the population changes have failed. Chitty (1952) has suggested how random variations in weather might tend to correlate cycles: in widespread favourable years, peak populations which had already approached their maximum densities might be unable to reach much higher levels; whereas sparser populations would be increasing rapidly towards the maximum possible for each particular environment—thus all populations would tend to approach their respective

peaks together. On the other hand, if a widespread spell of severe weather were to result in mortality rates which increased with population density, then all populations would be reduced to similarly low levels. The effects of these two extreme conditions should be the promotion of some degree of synchrony.

In conclusion, there is an obvious need in the future to determine the general periodicity in such places as Greenland and Spitsbergen; and to obtain more precise information for the Maritime Provinces, Alaska, and the intermediate areas between these two and the main part of Canada. But of greater importance is the need for quantitative data on changes in the populations of individual species in a number of particular localities where two or more fluctuating species occur together. It is perhaps by focusing our attention on restricted areas where the number of variables is less than in wide regions and where we can more precisely follow the changes in the populations of a number of species, that we may hope to find clues for the solution of this most difficult but fascinating problem.

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SUMMARY

A well-marked cycle in the numbers of tetraonid game birds occurs throughout most of the northern part of North America. Although in any one restricted district the length of the cycle may vary within fairly wide limits, there is a strong tendency over great areas for crashes to occur in synchrony every 9–10 years. In most of Canada and in the northern United States one main cycle appears to operate; however, in the Canadian Maritime Provinces the cycle seems to be advanced in its corresponding stages by about 3 years over the 'main' cycle, whereas in Alaska the cycle appears to be retarded by about the same interval.

In Britain and north-western Europe shorter general cycles prevail—with a mean length of about 5 years in Britain and 3–4 years in Finland and Scandinavia. Although the British and Scandinavian cycles have many peak years in common it is impossible to decide, on present data, whether or not these coincidences are random.

Fluctuations in abundance of tetraonid game birds also occur in Greenland, Iceland, the north-western U.S.S.R. and Spitsbergen. The Icelandic cycle seems to be predominantly a long one, showing resemblances to the North American pattern; whereas

the U.S.S.R. and Spitsbergen cycles are almost certainly short cycles of the British and Scandinavian type. More information is needed to characterize the Greenland fluctuations.

In North America the tetraonid fluctuations almost certainly occur in close synchrony with those of the snowshoe rabbit; in Scandinavia they appear to be connected with the lemming cycle. When populations of many very different species of animals fluctuate together the most likely synchronizing agent would seem to be a common weather system. There is no evidence in support of the hypothesis that an extraterrestrial factor is responsible.

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THE STATISTICAL ANALYSIS OF GAME-BIRD RECORDS. II

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In a preceding paper (Moran 1952) annual data on the bags of grouse, ptarmigan, capercailzie and blackgame on a number of Scottish estates from 1866 onwards were analysed to determine how far the populations of these birds tended to vary in unison. It was assumed that the number caught each year was a good indicator of the size of the population. No real evidence of oscillatory or 'cyclic' tendency was found, but all the series were definitely serially correlated. The correlations between the series are shown in Table 1.

Table 1. *Correlations between game-bird series*

	Ptarmigan	Caper	Blackgame
Grouse	0·504	0·504	0·347
Ptarmigan	—	0·417	0·052
Caper	—	—	0·189

The correlations between grouse, ptarmigan and caper were all shown to be statistically significant and also that between blackgame and grouse. This fact requires explanation. The four species are not, apparently, ecologically dependent, and it therefore appears of interest to inquire whether the correlation is due to the effect of weather conditions. In order to investigate this, the residuals from the serial regression formulae (for the first three species) were correlated with a selected series of meteorological data from Aberdeen.

The meteorological series chosen were taken from the World Weather Records (*Smithsonian Miscellaneous Collections*, vols. 79, 90 (1927, 1934) and are as follows:

A. May temperature, 1871–1930.
B. June temperature, 1871–1930.
C. May rainfall (mm.), 1871–1930.
D. June rainfall (mm.), 1871–1930.
E. Minimum of the average monthly temperatures for December, January and February of the winter preceding the bag, 1872–1930.
F. Mean rainfall (mm.) for August, September and October, 1871–1930.

To see how far these meteorological conditions were uniform over the area they were correlated with the same data for Edinburgh. The observed correlations were:

A	B	C	D	E	F
0·885	0·867	0·635	0·561	0·815	0·579

These values are all far beyond the 1% significance level in the absence of serial correlation from year to year. No test has been made of the latter which is very unlikely to exist. These figures indicate, therefore, that the Aberdeen values can be taken to represent the general variation about the mean over a wide area.

Serial correlations of the grouse, ptarmigan and caper series show clearly that these series are serially correlated. Instead of correlating the meteorological series directly with the observed bags, they have been correlated with the residuals from regressions of each year's bag on the previous years. Thus if x_t, y_t and z_t are the observed bags for the year t, the meteorological data were correlated with the residuals given by the expressions:

$$x_t - 18169 - 0{\cdot}643(x_{t-1} - 18169) \text{ (grouse)},$$
$$y_t - 105 - 0{\cdot}483(x_{t-1} - 105) \text{ (ptarmigan)},$$
$$z_t - 144 - 0{\cdot}592(x_{t-1} - 144) \text{ (caper)}.$$

The effect of this should be to increase somewhat the sensitivity of the test of meteorological effects. The meteorological series were correlated with the three series of residuals for the same year and also with the following year in order to test if there was a lag effect such as has been observed in similar investigations on the Canadian lynx (Moran, in press). The results of these calculations are shown below in Table 2.

Table 2. *Correlations of game-bag residuals with meteorological series*

	A	B	C	D	E	F
Grouse	0·125	0·005	−0·059	−0·097	−0·019	−0·129
Ptarmigan	0·148	0·062	0·156	−0·186	0·116	−0·152
Caper	0·318(*)	0·042	0·107	−0·141	0·286(*)	−0·165
Grouse (lagged)	0·210	0·098	−0·115	−0·239	−0·117	−0·443(*)
Ptarmigan (lagged)	0·117	−0·086	−0·183	0·002	−0·071	−0·197
Caper (lagged)	0·324(*)	−0·039	0·041	−0·148	0·173	−0·322(*)

The 5 % significance points for a correlation coefficient based on 59 and 60 pairs of observations are 0·2563 and 0·2541 and the 1 % points are 0·3328 and 0·3300. The individual correlation coefficients in the above table which, taken by themselves, would be judged significant at the 5 % level are marked with an asterisk. Care must be taken in ascribing reality to them since we have calculated thirty-six coefficients and some may well appear significant by chance.

Correlations with series B, C and D can clearly be dismissed. There is thus no evidence for the populations being dependent on May and June rainfall and on June temperature, lagged or unlagged. The correlations with series E (minimum winter temperature) are more interesting. There is some indication that caper is adversely affected by cold winters but the other species have correlations which are not significant and which are negative in three cases. Clearly any meteorological factors which may explain the synchronization of the population changes must have the same effect on all three species and the correlations must therefore be of the same sign. This is observed with series A (May temperatures) and F (rainfall in August, September and October). Only four of the twelve correlation coefficients are significant but the correlations with series A are all positive and those with series B all negative. Table 2 therefore provides some evidence that the bird populations are influenced by weather and this is particularly evident in the case of caper.

What we wish to know, however, is whether this dependence is large enough to account for the high correlations between the species given in Table 1. On the data used it seems that this is possible but by no means proved. For a full test we should

have to do a multiple regression of each series on all the likely meteorological factors and this would be a very large undertaking and would leave few degrees of freedom. Thus we cannot assert definitely that the synchronization is due to weather. However, for caper the dependence on weather is clear. The correlations with series A (0·318), with series A shifted one year back (0·324) and with series F shifted one year back ($-0·322$) are all high, and these three series can presumably be regarded as statistically independent.

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THE ECOLOGY OF *GAMMARUS DUEBENI* LILLJEBORG AND ITS OCCURRENCE IN FRESH WATER IN WESTERN BRITAIN

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(With 11 Figures in the Text)

CONTENTS

	PAGE		PAGE
Previous work on the biology of *Gammarus duebeni*	38	Factors controlling local distribution	64
Geographical distribution	40	Laboratory investigations	74
The theory of distinct fresh and brackish water races	47	Discussion	77
Food	55	Acknowledgements	80
The life cycle	56	Summary	81
		References	81

Tattersall (1913), Poulsen (1929), and Forrest, Waterston & Watson (1936) recorded *Gammarus duebeni* from freshwater habitats on small islands off the west coasts of Ireland and Scotland and the Faroes, and Reid (1939) showed that this species was widespread in the fresh waters of Ireland. As elsewhere it was known only from brackish coastal waters these records were of considerable interest. Jones (1948) showed that both *G. duebeni* and *G. pulex* Linn. occurred in fresh water in the Isle of Man, and that in one small river they occurred together. It was later shown (Hynes 1951) that records of *G. pulex* from Ireland were erroneous, and that the Isle of Man was the only place where the two species were known to occur together in fresh water. In view of this it was felt that investigation there might clarify the ecological relationship between them, and show why *G. duebeni* should penetrate far into fresh water only in these western islands. Several new problems have arisen in the course of this work, but much information has been collected on the ecology of *G. duebeni* and on the British distribution of this species and of *G. pulex pulex* (L.), and it forms the subject of this paper.

PREVIOUS WORK ON THE BIOLOGY OF *GAMMARUS DUEBENI*

Nearly all the published ecological work on *G. duebeni* refers to its occurrence in brackish water, but since its discovery in fresh water some work has been done on osmoregulation.

Sexton (1924) attempted to breed it in captivity in order to obtain a complete series of moults, but she found it unsuitable for this purpose 'because of its cannibal propensities'. She later (1942) reported that she kept the species in the laboratory in sea water, brackish water and fresh water.

Legueux (1924) recorded the species as common in supra-littoral brackish waters in northern France. She stated, from laboratory observations, that young females have no bristles on their oostegites. These appear later and persist for about three

ovipositions, after which a period of rest sets in, and they moult and lose the hairs, the positions of which, however, remain visible on the oostegites.

Meek (1929) recorded the species from a mine, into which it had apparently been washed by floods, but in which it seemed that breeding occurred. The specimens were transparent and apparently blind, but became normal in captivity.

Le Roux (1933) made a detailed laboratory study of the growth including the development of secondary sexual characters. Her shrimps were about 1·9 mm. long at hatching; and in 10% sea water on a mixed diet they matured at the thirteenth moult when 80–90 days old.

Elmhirst (1935) showed that specimens from brackish water voluntarily entered layers of fresh water in the laboratory, whereas two purely marine species avoided them.

Reid (1939) recorded the species from many freshwater localities in Ireland, including many far inland and at considerable altitudes. He tried to breed brackish water specimens from southern England in fresh water without success, and, although he could find no morphological differences between freshwater and brackish water specimens, he suggested that they might belong to different physiological races.

Beadle & Cragg (1940*a*) found that brackish water specimens could live in 2% sea water but maintained a higher blood chloride level there than did *G. pulex*, which could not stand high concentrations of sea water. Later (1940*c*) they showed that *G. duebeni* from fresh water lived longer in distilled water than specimens from brackish water, which lost salt rapidly and died. Beadle (1943) pointed out that in some streams *G. duebeni* has penetrated far in fresh water, while in others (e.g. in the Inner Hebrides, Beadle & Cragg 1940*b*) it occurs for only a few feet above sea-level despite the absence of competing species. He suggested the possibility of two genetically distinct populations.

Cheng (1942) showed that in brackish water in Anglesey the species breeds in winter and spring, but he obtained no samples at other seasons. He found that in general the larger females carried more eggs than the smaller ones.

Segerstråle (1946), in the first large field study of the species, found that in Finland it occurs primarily in rock-pools and can tolerate a wide range of salinity from 1 to 85‰, although becoming immobile at the higher salinities. Later (1950) he attributed its absence from truly marine localities in the Baltic to competition with *G. zaddachi* Sexton.

Forsman (1948, 1951) extended Segerstråle's investigations in field and laboratory. His animals did not breed in tap water, but the life cycle was normal in sea water of salinity between 25 and 35‰. He suggested that the restricted distribution was due to competition.

Kinne (1952*a*, *b*) investigated the life cycle in a brackish lake at Kiel, and studied the animals' growth in the laboratory. He found that reproduction occurred chiefly in late winter and early spring, and that the sex ratio varied owing to an effect of temperature on sex determination. In a later paper (1952*c*) he studied osmoregulation, heart-rate and oxygen consumption at different salinities and temperatures. In a fourth paper (1953) he showed that the winter resting period was influenced by a fall in

temperature but could not be fully explained by the seasonal temperature cycle. He also studied the number of eggs carried by females of different sizes at different times of year.

GEOGRAPHICAL DISTRIBUTION

(*a*) *Published records*

G. duebeni has been recorded from brackish-water habitats on the European mainland from Kanin, Northern Siberia, the White Sea coast (Segerstråle 1948), the Murman coast (Stephensen 1940*a*), Petsamo (Segerstråle 1948), Norway (Sars 1895), Sweden (Forsman 1951), Finland (Segerstråle 1946), Denmark (Stålberg 1940), Germany (Sexton 1942, Kinne 1952*a*), Holland (Redeke 1937), and Northern France (Pacaud 1944) and from the Black Sea (Stephensen 1940*a*). It has also been recorded from brackish water in England, Scotland and Ireland (Spooner 1947), the Isle of Man (Jones 1948), the Inner and Outer Hebrides (Nicol 1936, Forrest *et al.* 1936 and Beadle & Cragg 1940*b*), the Orkneys (Nicol 1938, Reid 1943), the Shetlands (Walker 1914), the Faroes (Stephensen 1928) and Iceland (Stephensen 1940*b*), and from warm brackish springs in Greenland (Stephensen 1917). It does not appear to occur in Spain, as, although Margalef (1944) recorded it there, he later (1948*a*) stated that the species he had found was *G. locusta aequicauda* Martynov. From this distribution it would appear that the record from the Black Sea requires confirmation, especially as Caspers (1951), who has recently made an extensive study of the fauna, did not record it.

The species has been recorded from fresh water from Cape Breton Island, Gulf of St Lawrence, Canada (Shoemaker 1930), Iceland (Poulsen 1939) and in a hot spring there at 10·3–25° C. (Tuxen 1944), the Faroes (Poulsen 1929), the Shetlands (Stephensen 1928), Barra, Outer Hebrides (Forrest *et al.* 1936), the Inner Hebrides (Beadle & Cragg 1940*b*), the Isle of Man (Jones 1948, Hynes 1950), Ireland (Reid 1939, MacDonald 1946), Anglesey and western Cornwall (Crawford 1937). There is some doubt whether or not some records from the Kanin peninsula, Siberia (Segerstråle 1948) were from fresh water, but the localities were near the sea, and the species is known to be able to penetrate fresh water for a short distance in France (Pacaud 1945).

(*b*) *Distribution in Britain*

With the collections made by or for me and information supplied by others the maps shown in Fig. 1 have been prepared. These maps are based only on specimens identified by the late Dr Stephensen, Dr Spooner, Mr Crawford, Mr Reid, Mr Fryer, Mr MacDonald and myself, and show the distribution, on the vice-county system, of *G. pulex* and *G. duebeni* in fresh water. No use has been made of other records of *G. pulex*, as it is not always possible to be sure of the identifications, but without using any dubious records it has been possible to obtain information from most of Britain. In addition to the vice-county records small arrows on the maps indicate small islands where the two species have been found in fresh water.

G. duebeni has also been similarly recorded from brackish water in the following vice-counties: Shetland, Orkney, N. and S. Sutherland, Caithness, Hebrides, W. Ross, W. Inverness, N., Mid and S. Ebudes, N. and Mid Perth, S. Perth and Clackmannan, Argyll Main, Forfar, Bute and Arran, Kinross and Fife, Renfrew, Ayr, Antrim,

Fermanagh, Down, Dublin, Clare, Wexford, Waterford, E. and W. Cork, Isle of Man, Anglesey, Caernarvon, Carmarthen, N. and S. Northumberland, Cumberland, Westmorland and N. Lancs, Mid- and S. Lancs., E. Yorks, Cheshire, E. Norfolk, E. Suffolk, N. and S. Essex, E. Kent, W. and E. Cornwall, N. and S. Devon, S. Hants and W. Sussex. It is thus reasonable to suppose that the species occurs in suitable brackish habitats all around the coasts of Britain, and that it only lives in fresh water in the west. There it is found far inland, as is shown by its extended distribution in Ireland, over all of which it probably occurs.

G. pulex appears to occur almost all over the British mainland, but not on islands off the coast. The few exceptions to this are Oban Island, the Isle of Man and Skomer,

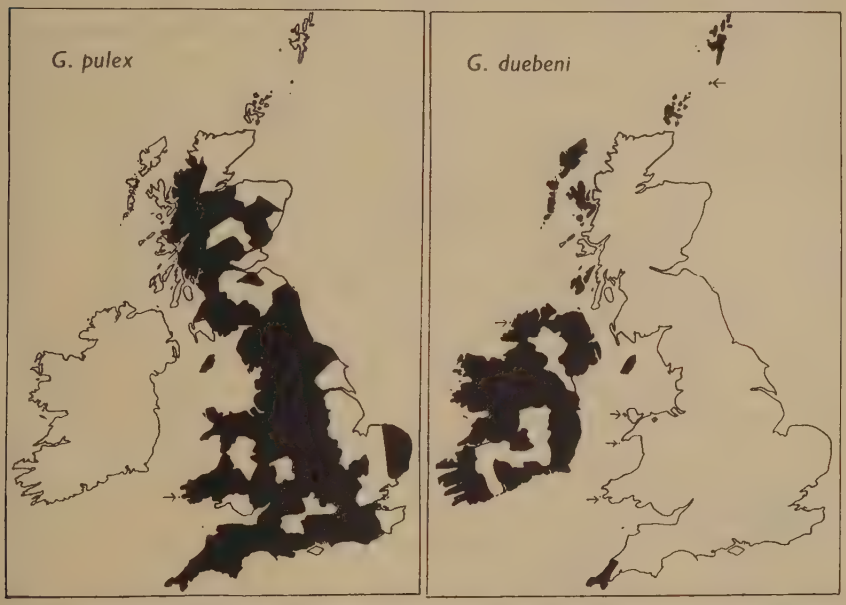

Fig. 1. Distribution of *G. pulex* and *G. duebeni* in the British Isles. Records are shown by vice-counties, but in addition arrows indicate small islands on which the species also occur.

and it is of interest to note here that *G. duebeni* occurs on Skokholm only a few miles from Skomer. No information has been obtained about the freshwater Amphipoda of the Mid Ebudes, Bute, Arran and the Clyde islands, Lundy, the Scillies and the Isle of Wight. It seems probable that further collecting would reveal the presence of *G. pulex* throughout England, Wales and S. and Mid Scotland, and probably the Isle of Wight also, but there are indications that it really is absent from the extreme north of Scotland (Reid 1951), and collections made there for me have all contained only *G. lacustris* Sars.

G. duebeni has been recorded from Anglesey (Crawford 1937), but as is shown below these records refer not to Anglesey itself, but to Holy Island. Similarly, it has been reported from fresh waters near the coast of Sutherland and W. Ross. Through the kindness of Mr Reid, Dr Macan and Mr Munro I have been able to ascertain that in

every such locality from which water samples could be obtained the salinity was high, ranging from 158–3480 mg.Cl/l. These localities must therefore be classified as brackish.

On the whole, therefore, it can be stated that on any island in Britain *G. duebeni* occurs only in brackish water unless *G. pulex* is entirely absent. Where *G. pulex* is present *G. duebeni* is not found in fresh water. The two exceptions to this rule (W. Cornwall and the Isle of Man) are discussed in detail below.

(*c*) *Distribution in the Isle of Man*

Except in the north where it is flat and swampy, the Isle of Man is rocky and mountainous, and there are numerous swift rivers and streams. In the lower reaches, where they cross agricultural land, many of them flow more slowly, but almost all

Fig. 2. Distribution of *G. pulex*, *G. duebeni* and *G. zaddachi* in the southern half of the Isle of Man. No *Gammarus* were found in fresh water north of the area shown. Results shown as P = *G. pulex*, D = *G. duebeni* in fresh water, B = *G. duebeni* in brackish water, Z = *G. zaddachi*, O = localities without *Gammarus*. The numbers identify the separate streams.

remain sufficiently swift to have stony substrata. A preliminary account of the freshwater Amphipoda has already been published (Hynes 1950). Fig. 2 is a map of the southern half of the island showing all the permanent streams, the localities which have been investigated, and the occurrence of Amphipoda in fresh and brackish water. No *Gammarus* were found in fresh water anywhere to the north of the area shown on the map, although almost all streams there were investigated, and many appeared to offer suitable habitats.

G. zaddachi zaddachi Spooner was found at the mouth of all but one of the larger streams, including the Sulby river, which is north of the area covered by Fig. 2, and in

the one estuary where it was not found no Malacostraca appeared to be present, possibly because of pollution. This species was not found anywhere above the highest level of spring tides. This distribution is therefore fully in accord with the findings of Spooner (1947).

G. duebeni was found in three distinct types of locality: freshwater streams, rock-pools with freshwater seepage at or just above high spring-tide level, exactly as described by Forsman (1951), and on stony beaches at the mouths of small streams down as far as high neap-tide level. The species was not always present in the last type of locality, and no explanation was found for this, but in suitable rock-pools it was always present, and usually abundant, and, as it was found in several pools north of the area covered by Fig. 2, it probably occurs in such habitats all round the island.

G. pulex was found abundantly in two rivers and five small streams, and in one of each it occurred together with *G. duebeni*.

The distribution of both *G. duebeni* and *G. pulex* in fresh water is therefore peculiar. The former is confined to the southern quarter of the island, but even there was absent from many streams, while the latter occurs in scattered localities in the southern half of the island. A few of the streams in which no amphipods occurred were possibly not suitable, either because they were too torrential or sluggish and muddy, but the great majority appeared to be suitable, and are certainly permanent. In the smaller streams, up to about 2 m. across, where the current was moderate, the shrimps were found under stones and amongst vegetable debris all over the stream-bed, but in the larger streams and small rivers, several metres across and with a swift current, they occurred only in submerged grass, etc., at the edge, out of the main force of the current. During periods of low water or where there was shelter in midstream, in the form of beds of *Callitriche* or moss, *Gammarus pulex* at any rate was found far out in the river-bed. This is in agreement with the statements made about *G. pulex* by Wundsch (1922). As two Manx streams, the Silver burn, which is about 10 m. wide for most of its course, and the Crogga river, which is only 2–3 m. wide, are the only localities where *G. pulex* and *G. duebeni* are known to occur together in fresh water they were examined in detail.

In the Silver burn (Fig. 2, no. 19), where 1360 specimens were collected from ten stations, at high neap-tide level 100% of the specimens found were *G. zaddachi*; between there and the upper limit of spring tides 90% were *G. zaddachi*, 9% *G. duebeni* and 1% *G. pulex*; at high spring-tide level the figures were 56, 8 and 36% respectively. Above this point *G. zaddachi* was absent, and *G. duebeni* rose to 18% of the population but fell steadily within the next kilometre to 4%. Three and a quarter kilometres from high spring-tide level 2% of the population was *G. duebeni* and the rest was *G. pulex*. At that point a small tributary enters the river beside a twelfth-century bridge. This stream is led over a small artificial water-fall about 1 m. high and then canalized alongside the bridge for about 20 m. before entering the river. Presumably this fall was made when the bridge was built, to prevent undercutting. Above the fall was a pure population of *G. duebeni*, while below it 98% of the specimens were *G. duebeni* and 2% were *G. pulex*. In the river itself above the bridge only *G. pulex* was found. About 300 m. above the bridge a medium-sized tributary enters on the left bank, and *G. pulex* was traced up this for

about 800 m., although it was absent about 4 km. above the junction. In the main stream *G. pulex* was found amongst *Fontinalis* for about 100 m. above the junction, but it was absent farther upstream. In the tributary moss and other shelter occurred almost continuously along the stream, whereas in the main river shelter was much sparser, and above the highest point at which *Gammarus pulex* was found there was a reach of about 100 m. of swiftly flowing water devoid of vegetation. Above this reach moss again occurred, and was abundant in places, but no *Gammarus* were found.

The Crogga river (Fig. 2, no. 23) has much moss and submerged grass, and at its mouth fans out over a gravel beach. Here few *Gammarus* were found although both *G. pulex* and *G. duebeni* were present. Upstream for about 400 m. both species were found sparsely, *G. pulex* being the commoner. At this point a small tributary enters on the left bank, and in this *G. duebeni* was absent and *G. pulex* was abundant. This stream flows from near the watershed of the Douglas river in which *G. pulex* is also abundant. Above the tributary for about 500 m. only *G. duebeni* was found sparsely, and farther upstream no *Gammarus* occurred. At the point where *Gammarus* ceased to occur a very small tributary enters on the right bank, and in this *G. duebeni* was abundant. No specimens could be found even a short distance above the tributary, nor on the left bank of the main stream for about 20 m. below it. It can be seen, therefore, that although both species can be collected at the same loci in parts of these two streams their occurrence together is not a simple phenomenon.

As *G. duebeni* did not occur throughout the whole length of some streams, two of these were also investigated in detail in an attempt to find what factors limited its distribution. Poyllvaaish stream (Fig. 2, no. 18) is small and stony at its mouth where it fans out over a rocky beach. Here *G. duebeni* was very abundant, and it occurred upstream under stones and amongst vegetation for 1·4 km. Farther upstream the species was absent, but this appeared to be because the stream was sluggish and muddy. Arbory stream (Fig. 2, no. 17) is also small. *G. duebeni* was common at its mouth and in much of the main stream, and of its four tributaries three contained large populations, but one and the upper part of the main stream were without the species. The one tributary is very small and may dry up at times, but the upper part of the main stream is permanent and appeared to be an ideal habitat. In contrast, however, to the Crogga river the species was found for a few yards above the uppermost tributary in which it occurred abundantly. This would seem to indicate that the water itself was suitable, but that some other factor prevented further spread upstream. There was no obvious barrier such as a waterfall, and no indication that the current was stronger than in streams in which the species is abundant.

It is clear therefore that the distribution of *G. pulex* and *G. duebeni* in the island is difficult to explain. The chief problem is the absence of *G. duebeni* from many apparently suitable localities. It appears to occur all round the coast, and so presumably has access to all streams, and that it can penetrate streams in which it does not normally occur was shown by the capture, on 1 January 1951, of a single adult male in Glenchass stream (Fig. 2, no. 13) about 200 m. from the sea, at an altitude of about 50 m. This little stream was repeatedly searched both before and after that date, and was certainly without a population of *G. duebeni*: the specimen must have climbed a 20 m. cliff to reach the point at which it was taken.

The distribution of *G. pulex* is perhaps explained by assuming that it has only recently been introduced into the island, possibly with young trout from hatcheries on the mainland. It was found in only six drainage basins, three of which—the Silver burn, the Neb (Fig. 2, no. 2), and the Douglas (Fig. 2, no. 24)—are well-known trout streams. Of the three others, one (the Crogga river) is close to a tributary of the Douglas, from which it has possibly spread by natural means, and another flows through the grounds of Government House, where there are still the remains of a fish pond, which may have been stocked with fish. The third (Ballagyr stream, Fig. 2, no. 1) is close to tributaries of the River Neb, and may also have received its population by natural spread. The suggestion that *G. pulex* is a recent introduction is supported by its distribution in the Silver burn, where it would appear to be slowly spreading upstream and not yet to have got up the twelfth-century waterfall. Its absence from some parts of the watershed of the Douglas river is possibly because these are swift and turbulent, and restrict the spread of the species, and the same may apply to the Crogga river and the main stream, and hence many tributaries, of the River Neb. Strong evidence of recent introduction is also supplied by the fact that it was possible to establish the species in a stream in the south of the island: this is discussed more fully below.

Fig. 3. Distribution of *G. pulex* and *G. duebeni* on the Lizard peninsula. Lettering as Fig. 2.

(*d*) *Distribution in West Cornwall*

G. duebeni was first reported from the Lizard peninsula by Crawford (1937) who examined collections made by Dr Kitching. I visited this area in August 1952, and was able to extend Dr Kitching's observations. Fig. 3 shows the distribution of freshwater Amphipoda in this area. *G. duebeni* was found in all streams investigated on the south-western tip of the peninsula and was absent elsewhere, and *G. pulex* was found in only a few streams near the narrow isthmus between the Helford river and

the Loe. The former is a muddy tidal creek, and the latter, from the map, was presumably similar until relatively recently. Nowhere were the two species found together. This is apparently the most westerly point in England in which *G. pulex* occurs. All reasonably accessible streams between the Loe and Lands End, and round to St Ives and the Red river at Camborne, were carefully searched, and no amphipods were found, although most of the streams appeared suitable.

It is suggested that here, as in the Isle of Man, *G. pulex* may be a recent immigrant, and has only recently entered the peninsula via the isthmus. If so, it may be expected to spread southwards until it comes into contact with *G. duebeni*. As in the Isle of Man also, there appears to be some factor other than general physiography which prevents the colonization of some empty streams by *G. duebeni*. A point of interest is that in one stream in the north of the peninsula, Mawgan creek (Fig. 3, no. 25), *G. duebeni* was found at the mouth and for a distance of about 250 m., up to a height of about 8 m. O.D., but was unaccountably absent farther upstream. In all the loci, both there and elsewhere, where *Gammarus* occurred it was abundant.

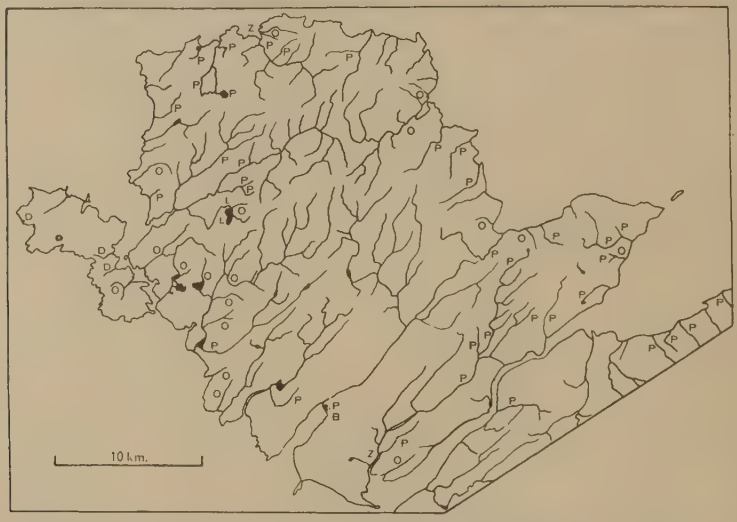

Fig. 4. Distribution of *G. pulex*, *G. duebeni*, *G. lacustris* and *G. zaddachi* in Anglesey. Lettering as Fig. 2, L = *G. lacustris*.

(*e*) *Distribution in Anglesey*

G. duebeni was recorded from fresh water in Anglesey by Crawford (1937), and Prof. Cragg has also collected it there. In January 1950 I investigated over fifty apparently suitable streams on the island, Holy Island and the neighbouring mainland. The results of this survey, and data kindly supplied by Prof. Cragg, are shown in Fig. 4. In addition to the information given on the map Prof. Cragg also found specimens of *G. duebeni* near the mouth of two streams on Anglesey, but in one they ranged for only 200 m. above high-water mark, and in the other only 25 m. These records cannot therefore be regarded as certain records from fresh water (cf. Mawgan creek, above). The record of *G. zaddachi* was also very near to the sea.

It can be seen from the map that all the other records of *G. duebeni* from fresh water were not from Anglesey itself, but from Holy Island, and that *G. pulex* was not found there. This is therefore another example of vicarious distribution of the two species. The salinity of two of the Holy Island localities was, in January 1950, higher than that in any of the streams sampled on Anglesey itself (122 and 158 mg. Cl/l.), but the salinity of the stream on Holy Island where no *Gammarus* was found was of the same order, and many of the Anglesey streams had salinities within the range in which *G. duebeni* occurs in the Isle of Man. It is certain therefore that it is not salinity which controls the distribution of the species. This is discussed more fully below.

(*f*) *Distribution in Ireland*

Fig. 1 shows that *G. duebeni* has been found in most vice-counties of Ireland, and it is probable that further collecting would reveal its presence in all. It is recorded from rivers, streams and lakes, but its occurrence is not universal. Frost (1942) did not find it in the acid waters of the River Liffey at Ballysmuttan, although it was common farther downstream in the alkaline waters at Straffan, and has been found in Pollaphuca Reservoir only a few miles below Ballysmuttan. It is also absent from other areas in the Wicklow Mountains. Dr Frost failed to find it in Lough Dan and Glenda Lough, and in nearby streams flowing into the Avonmore river, and Dr J. W. Jones has also unsuccessfully searched this area. Similarly, Dr Frost failed to find it in the River Dargle at Bray. She has suggested to me that in Wicklow the species is associated with limestone and calcareous glacial drift, and it may be that waters where it is absent are too soft. It is difficult, however, to reconcile this explanation with the fact that many Irish records are from waters of low pH (Reid 1939); perhaps the acidity of these waters is not directly related to their calcium content. In any event the widespread distribution of the species in Ireland shows that it can maintain itself in many types of fresh water far from the sea, and that it is not dependent on blown sea-spray or saline waters. That sea-spray might be a factor of some importance is suggested by its presence in fresh water elsewhere only on small islands or on the southern extremities of larger islands.

(*g*) *Distribution in Fair Isle*

Mr Stout, who collected specimens of *G. duebeni* for me in Fair Isle, states that the species is frequent in the streams and wells in the south-west of the island, but absent from the hilly north-east end. This is yet another area in which it is confined to country with a south-westerly aspect.

THE THEORY OF DISTINCT FRESH AND BRACKISH WATER RACES

In order to test the suggestion that *G. duebeni* exists in two distinct physiological races various experiments and observations were made.

(*a*) *The ability to interbreed*

It was found that specimens from a stream and from a beach mated readily in the laboratory in 20 % sea water, and the offspring of a female from a stream, unconnected with any brackish water population (Fig. 2, no. 9), and a male from a beach, in the

stream above which no population occurred (Fig. 2, no. 15), were normal and fertile. Some of the F_2 generation were successfully back-crossed with stream specimens, and the rest produced an F_3 generation. Similarly, males from the same stream were successfully crossed with females from a rock-pool, and vice versa, and the offspring were normal and fertile.

In view of the fact that, as Beadle (1943) has also observed, continuous populations, from fresh to brackish water, occur in the field this readiness to interbreed suggests that there is no genetical difference between the two types of population. Presumably if such a difference did exist some reproductive barrier would prevent the wastage of cross-breeding. It is, however, possible that a genetic system such as that discovered by Heuts (1947) in *Gasterosteus aculeatus* L. has been evolved, which enables some crossing to occur without loss of physiological adaptation of the offspring to one or other of the habitats.

(*b*) *Osmoregulation*

Beadle's (1943) work suggests that there should be a clear distinction between the time for which specimens from fresh and brackish water can survive in distilled water. This has not been found to be so.

Several experiments were made in which specimens, usually adult males, from the two types of habitat were washed twice in glass-distilled water, and kept individually in small jars in 10–30 ml. of glass-distilled water, which was changed every 24 hr. Control shrimps lived for weeks in stream water under similar conditions without food. The distilled water used was not toxic as shrimps lived through two generations in such water to which 20% of sea water had been added.

The results of the experiments varied considerably and were quite inconclusive. The findings were briefly as follows:

Exp. 1. Ten specimens from a stream lived from 1 to 7 days, mean $4{\cdot}0 \pm 0{\cdot}71$; 10 specimens from a beach lived 2–5 days, mean $3{\cdot}2 \pm 0{\cdot}42$. Not significant ($P > 0{\cdot}05$).

Exp. 2. Ten specimens from a stream lived 1–6 days, mean $3{\cdot}0 \pm 0{\cdot}46$; 10 specimens from a rock-pool lived 1–3 days, mean $1{\cdot}9 \pm 0{\cdot}22$. This was the only experiment in which a significant result was obtained.

Exp. 3. Six specimens from a stream were alive after 4 days, while 6 from another stream, and 6 from a rock-pool were all dead within one day.

In these three experiments the specimens were transferred directly from stream water or 20% sea water, according to their origin, into distilled water.

Exp. 4. Ten specimens from each of three habitats were divided into batches of 5, one of each of which was kept in fresh water, while the other was kept in 20% sea water for 10 days. All were then placed in distilled water and the number of dead noted at intervals. After 24 hr.: stream A, 1 dead; stream B, 6 dead; rock-pool, 6 dead. The different pre-treatments of the specimens were without apparent effect.

Exp. 5. Specimens of five different origins were kept for 2 weeks in 2% sea water and then 6 specimens of each were placed in distilled water. The number of dead was noted every few hours. After 24 hr.: stream, 5 dead; rock-pool, 3 dead; laboratory-bred stream origin, 5 dead; laboratory-bred beach origin, 5 dead; laboratory-bred rock-pool origin, 6 dead. The laboratory-bred specimens had been reared in 20% sea water.

In Exps. 4 and 5 the amount of chloride in the distilled water after the first 6 hr.

was determined by titration. The water was poured off and renewed, and the titration was made with silver nitrate to a standard end-point, using a 1 ml. burette. At the end of the experiment the specimens were blotted and weighed. No correlation was found between the amount of chloride lost per unit of body-weight and the origin of the specimens or their final survival.

Exp. 6. Specimens were kept for 5 weeks in 20% sea water, and were then transferred to distilled water, which was changed after 24 hr. There were 11 specimens in each group. After 6 hr., 2 specimens from stream B were dead, but those from stream A and a rock-pool were alive and active. After 30 hr., 10 specimens from stream B and 6 from the rock-pool were dead. After 50 hr., when the experiment was discontinued, only 1 specimen from stream B and 2 from the rock-pool were alive, and they were very weak; all the specimens from stream A were alive and active. In this experiment, as in all others, death was preceded by swelling of the gills, which became globular and bright blue. This has also been observed by Kinne (1952*c*).

Exp. 7. Specimens were kept for 3 weeks in 2% sea water and were then transferred to distilled water. After 46 hr., 12 out of 24 from a stream, 22 out of 24 from a rock-pool, 10 out of 17 laboratory-bred rock-pool origin and 3 out of 9 laboratory-bred beach origin were dead.

The results of these experiments do not show a clear distinction between specimens of freshwater and brackish-water origin, but they do indicate that considerable differences can occur between different populations from the same type of habitat. Prof. Beadle has informed me that the specimens used for his work had been transported a long way, and had received different treatments. It seems therefore that his conclusion requires revision, and that there is in fact no physiological distinction between freshwater and brackish-water races of *G. duebeni*.

Forsman (1951) found that his rock-pool specimens would live much longer in distilled water than those noted above; he quotes periods of 17 days and 2–3 weeks. It seems possible that his experiments were made at lower temperatures. Forsman also showed that specimens from brackish water could survive great increases in salinity, and only became comatose at salinity 81‰ (equivalent to 44·8 g. Cl/l.) when placed in sea water which was allowed slowly to evaporate. This experiment was repeated with 25 male specimens from a rock-pool and from a stream respectively, which were placed, with food, in dishes of sea water. After 4 days, evaporation was allowed to occur, and 8 days later a few stream specimens died, the chlorosity then being 25·00 g. Cl/l. Three stream specimens remained fairly active for a further 3 days, after which the chlorosity was 29·40 g. Cl/l., but all were dead when the chlorosity reached 35·40 g. Cl/l. The rock-pool specimens lived a little better, and did not begin to die until the chlorosity was more than 26·81 g. Cl/l. More than half were still active 14 days after evaporation had begun and the chlorosity had reached 29·60 g. Cl/l. Two days later the chlorosity was 36·20 g. Cl/l., and the 11 surviving specimens were all comatose or extremely weak. This experiment is in general agreement with that of Forsman, although no specimens survived salinities as high as 81‰. It also indicates a slight difference in toleration between specimens from fresh and brackish water. This difference was, however, just as possibly due to the history of the individuals as to anything in their genetical constitution.

(*c*) *The antennal gland*

Beadle (1943) suggested that morphological study of the antennal gland of *G. duebeni* might show differences between specimens from fresh and brackish water, such as had been shown by Schwabe (1933) between *G. pulex* and *G. locusta* L.

This gland lies in the basal segment of the antenna, and consists of a thin-walled reniform end-sac, from which runs a convoluted tube opening at the tip of a conical projection on the lower distal margin of the segment (Cussans 1904). The walls of the tube, which runs through spongy tissue full of blood, consist of large cells whose protoplasm stains deeply with eosin. The walls of the end-sac and of the distal part of the tube in the antennary cone are not eosinophil. Presumably the eosinophil tissue is concerned with the resorption of salts from the urine.

In serial sections through the antenna it is possible to trace the course of the tube, and to obtain an estimate of its length. This was done for several specimens. Sections were cut at 5 μ and every fifth section was drawn on tracing paper with a projector at a magnification of $\times 100$. The total length of the eosinophil portion of the tube was then estimated by following it in its winding course through the drawings, and measuring the distance between the centre of the tube from one section to the next. This method was found to give reproducible results to within 0·2 mm.

Four specimens of *G. duebeni* were sectioned, a male and a female from a rock-pool and a male and a female from a stream, and a male and a female of each of *G. pulex* and *G. locusta* were also cut for comparison. The females were all between 10 and 11 mm. long, and the males between 12 and 13 mm. The lengths of the eosinophil portions of the left antennal glands were found to be as follows:

	Male (mm.)	Female (mm.)
G. locusta	1·6	0·9
G. duebeni from rock-pool	3·0	2·5
G. duebeni from stream	3·1	2·7
G. pulex	4·0	3·3

It was noted that the courses followed by the tubes were irregular, and not in regular loops as implied by Cussans and Schwabe, that the diameter of the lumen varied considerably along its length, and that the histological appearance of the wall was similar in all specimens.

The lengths given above show clearly that the tube is longer in *G. pulex* than in *G. duebeni*, and much longer than in *G. locusta*. This is in full agreement with the findings of Schwabe, and of Beadle & Cragg (1940*c*) that *G. pulex* has a more efficient osmoregulatory system than *G. duebeni*. They also indicate that there is no great difference between the tubes in the freshwater and brackish-water specimens of *G. duebeni*. Such difference as was found was within the unavoidable margin of error in making the measurements.

(*d*) *Size*

It was found that the males from Port Erin stream tended to be much larger than those from Gansey beach (Figs. 5, 6), and although large males were also found in some rock-pools (Fig. 7) it seemed possible that there might be a size difference between

brackish and freshwater populations. As it was not possible morphologically to distinguish when males were sexually mature this could not be carried further, but in the females full development of the oostegites made determination of sexual maturity simple. Accordingly, all the mature females from several collections were measured, as described below (p. 57), to the nearest millimetre, and their mean sizes were compared. The results are summarized in Table 1.

It was found that the mean lengths of females from rock-pools and from four streams were not significantly different from one another at $P < 0{\cdot}05$, but that the mean lengths of the specimens from the rock-pools and from Port Erin stream were highly significantly greater ($P < 0{\cdot}01$) than those from Gansey beach. The lengths of the females from the two beaches studied were also highly significantly different. It is clear therefore that, although significant differences in mean length of female do exist between populations, they are not correlated with the salinity of the habitat. The rock-pools were definitely brackish, and the two beaches were very similar in appearance and situation.

Table 1. *Mean lengths, with standard errors, of mature females of* Gammarus duebeni *from various Manx localities*

(The letters A to G have been given to the localities to simplify the last column of the table, where differences are shown as significant where P is less than 0·01, unless otherwise stated. The stream numbers are those shown in Fig. 2.)

Stream no.		Locality	Collections made in	No. of specimens	Mean length (mm.)	Significantly different from
9	A	Port Erin stream	All months	623	$10{\cdot}87 \pm 0{\cdot}121$	E, F
17	B	Ballagarmin stream	Jan.	45	$10{\cdot}88 \pm 0{\cdot}401$	F
17	C	Ballabeg stream	Jan.	87	$10{\cdot}57 \pm 0{\cdot}224$	F
10	D	Harbour Master's stream	Jan.	114	$10{\cdot}57 \pm 0{\cdot}322$	F
15	E	Gansey beach	All months	599	$10{\cdot}47 \pm 0{\cdot}117$	A, F, G (P 0·05)
18	F	Poyllvaaish beach	Jan.	82	$9{\cdot}20 \pm 0{\cdot}238$	All
—	G	Rock-pools, Scarlet Point	Jan. and Apr.	163	$11{\cdot}19 \pm 0{\cdot}285$	E (P 0·05), F

It could be argued that as the samples were not all taken at the same season they were not strictly comparable, but the samples from Port Erin stream and Gansey beach were taken in all months, and reference to Figs. 5 and 6 shows that there was no noticeable seasonal variation in the size of the mature females. This is, incidentally, in distinct contrast with the findings of Clemens (1950) on *G. fasciatus* Say in Lake Erie, who found a clear reduction in the size of the mature females during the breeding season: this he correlated with temperature, the females maturing at smaller size in warmer water.

It would seem definite therefore that the mean length of adult females and probably of males also, cannot serve to distinguish between brackish and freshwater races of *G. duebeni*, although differences in mean length do exist between populations. It may also be noted here that Prof. Kaj Berg and I, working in Denmark, found similar differences between mean length of adult females in populations of *G. p. pulex*, which we were unable to correlate with biological, chemical and physical features of the streams in which they occurred.

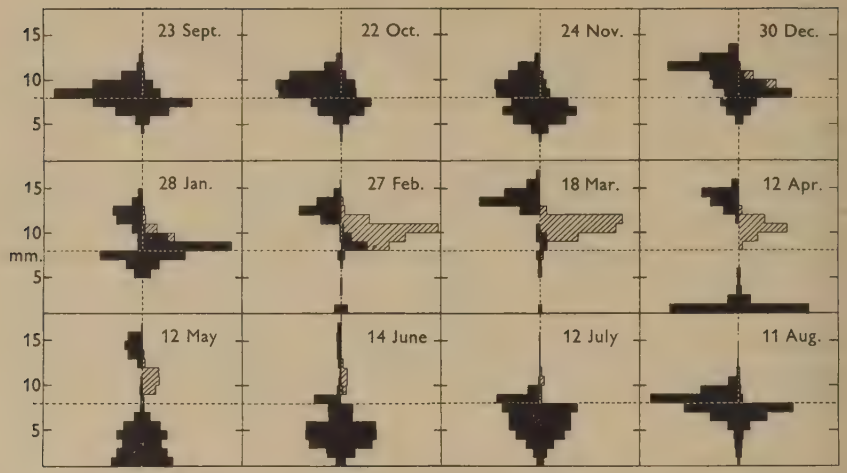

Fig. 5. Size and sex-distribution in monthly samples of *G. duebeni* from Gansey beach, 1949–50. The length of the shrimps is given by the vertical scale, and the length of each horizontal size-group block represents the percentage of the total in that size-group. The horizontal dotted line (at 8 mm. length) shows the lower limit of sex distinction: below this line the blocks are centred; above it males are shown on the left and females on the right. Females shown by the cross-hatched areas had fully developed and bristled oostegites.

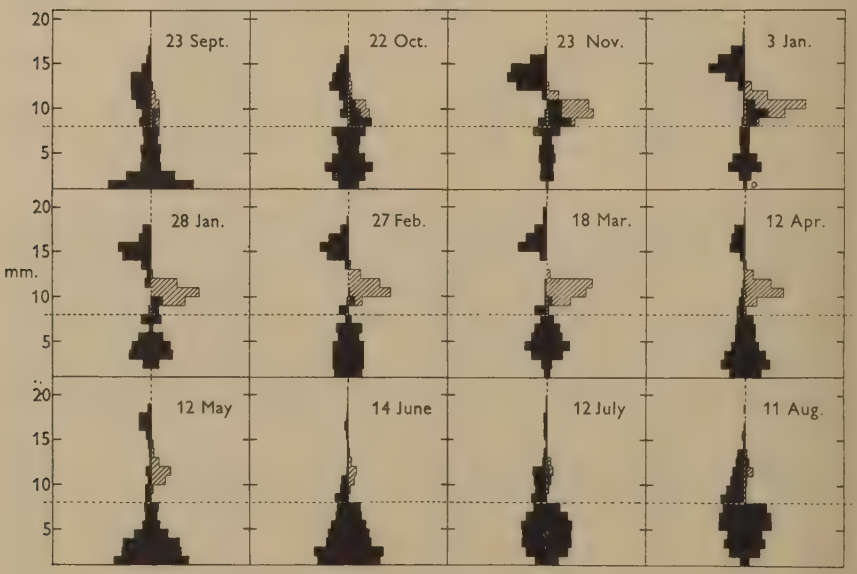

Fig. 6. Size and sex-distribution in monthly samples of *G. duebeni* from Port Erin stream, 1949–50. Arranged as in Fig. 5.

(e) Number and size of eggs

Cheng (1942) and Kinne (1952*a*) have shown that the number of eggs carried in the brood-pouch of *G. duebeni*, while being very variable, increases with the size of the female, and this phenomenon is known also in *G. fasciatus* (Clemens 1950). This was found to apply also to *G. duebeni* from the Isle of Man, as is shown in Table 2. In obtaining these results only females with unhatched eggs were examined as some of the young may leave the brood-pouch very soon after hatching. Also, because Kinne (1952*a*) has shown that in this species, as in *G. fasciatus* (Clemens 1950), the number of eggs per female varies with the season, only females collected during the height of the breeding season (January–April) were examined.

Inspection of the data indicated that in each size-group the mean number of eggs found in specimens from the beach and from the rock-pools was slightly higher than in the corresponding size-group from the stream. I am greatly indebted to Mr R. L. Plackett for statistical analysis of the data. His report was as follows:

An analysis of covariance suggests itself but this cannot be applied unless the variances are the same for different size-groups. An application of Bartlett's test to the beach data e.g. gave $\chi^2 = 27$ on 5 D.F., which is highly significant. To overcome this difficulty the square roots of the counts were noted, and as the variances of root-counts were homogeneous, the analysis was continued with these quantities.

A test was made of whether the regression coefficient of root-count on size could reasonably be supposed the same for the three localities.

Source of variation	Sum of squares	D.F.	Mean square
Between regression coefficients	2·3	2	1·15
Residual	110·9	255	0·43

This gives a variance ratio of 2·7, indicating that the coefficients may be pooled. An analysis of variance and covariance of root-count (y) and size (x) gave the following table:

		Sums of squares and products					
Source of variation	D.F.	x^2	xy	y^2	Sums of squares	D.F.	Mean square
Total	260	521·27	201·6	204·7	124·2	259	—
Localities	2	49·05	8·4	12·4	11·0	2	5·5
Within localities	258	472·22	193·2	192·3	113·2	257	0·44

This gives a variance ratio of 12·5, highly significant. The conclusion is that localities differ greatly in respect of number of eggs, adjustment being made for different size-ranges. In fact, adjusting mean root-counts to the values they should take when average female size is 11·5 mm. we get

Stream	$4{\cdot}168 \pm 0{\cdot}069$
Beach	$4{\cdot}332 \pm 0{\cdot}068$
Rock-pool	$4{\cdot}322 \pm 0{\cdot}078$.

The stream is significantly lower than the other two, which do not differ significantly.

It is clear, therefore, as might perhaps have been expected from physiological considerations, that, irrespective of size, the number of eggs laid by females in brackish water is greater than the number laid in fresh water.

It might also be expected that the eggs from the brackish-water specimens would be smaller than those from the freshwater specimens. All the eggs from each female size-group from Port Erin stream and Gansey beach were pooled, and from each batch

20 eggs were selected at random. The eggs are slightly oval, and the longest diameter was measured. There was no consistent difference in mean length of eggs from the different female size-groups from each habitat, but when the mean lengths of the 120 eggs from the two habitats were compared the following results were obtained:

Port Erin stream	$720{\cdot}3 \pm 6{\cdot}14\mu$
Gansey beach	$681{\cdot}5 \pm 6{\cdot}57\mu$

The difference between these means is highly significant ($P < 0{\cdot}01$) showing that, as anticipated, the eggs from brackish water were smaller, despite the great variability in the size of the eggs (Port Erin stream 540–860μ, Gansey beach 500–850μ), which is reflected in the large standard errors. Probably this variability in size was due to the different developmental stages of the eggs, although some may have been due to the effects of preservation. In any event both batches of females had been treated in the same manner.

Table 2. *Number of eggs per female in the brood pouches of specimens from three Manx localities*

(The females from each locality are divided into millimetre size-groups. Only females with unhatched eggs were used in compiling this table.)

Locality	Size group (mm.)	Number examined	Number of eggs		
			Max.	Min.	Mean
Port Erin stream	8–9	6	13	6	$10{\cdot}17 \pm 1{\cdot}26$
	9–10	20	18	4	$12{\cdot}35 \pm 0{\cdot}81$
	10–11	20	26	10	$17{\cdot}10 \pm 0{\cdot}84$
	11–12	20	28	14	$20{\cdot}65 \pm 0{\cdot}88$
	12–13	20	35	16	$24{\cdot}05 \pm 1{\cdot}26$
	13–14	4	44	22	$34{\cdot}00 \pm 4{\cdot}98$
Gansey beach	7–8	3	11	5	$7{\cdot}33 \pm 1{\cdot}87$
	8–9	20	20	3	$11{\cdot}50 \pm 0{\cdot}78$
	9–10	20	20	10	$14{\cdot}60 \pm 0{\cdot}61$
	10–11	20	26	10	$20{\cdot}75 \pm 1{\cdot}05$
	11–12	20	34	11	$23{\cdot}85 \pm 1{\cdot}63$
	12–13	9	37	9	$29{\cdot}33 \pm 2{\cdot}96$
Scarlet Point, rock-pools	8–9	5	20	10	$12{\cdot}00 \pm 2{\cdot}95$
	9–10	10	28	12	$19{\cdot}50 \pm 1{\cdot}50$
	10–11	20	27	10	$18{\cdot}60 \pm 1{\cdot}06$
	11–12	20	42	4	$21{\cdot}40 \pm 1{\cdot}67$
	12–13	20	39	17	$24{\cdot}05 \pm 1{\cdot}39$
	13–14	3	44	21	$30{\cdot}33 \pm 2{\cdot}21$
	14–15	1	—	—	42·00 —

The results of the investigations outlined above show that there are no substantial grounds for supposing that distinct brackish and freshwater races exist. It is true that there are some differences (e.g. in mean number of eggs), which seem to be correlated with salinity, but other differences, such as mean size of female, have been shown to be differences between populations. It has not been possible to confirm Beadle's findings that specimens from different salinities differ in their osmoregulatory ability, and while perhaps small differences in the antennal glands may exist it has not been possible to demonstrate them. This, together with the very scattered distribution of the 'freshwater race', often in very small populations (e.g. Bardsey and Skokholm), leads one to the conclusion that, although specimens from habitats of different salinities do differ in small respects, these differences are probably phenotypic. In theory this

could be readily confirmed by breeding experiments, but as is explained below, technical difficulties have so far rendered this impossible.

FOOD

Forsman (1951) states that in Swedish rock-pools *G. duebeni* feeds on any vegetable or animal matter available; and when the species was eliminated by frost *Enteromorpha* and various animals appeared which were not normally present, and which *Gammarus duebeni* was seen to attack and eat in the laboratory. Sexton (1924) found that cannibalism was prevalent in this species, and Macan (1950) suggests that it may be more carnivorous than other species.

The food of two other species of British freshwater *Gammarus* has been investigated. Haempel (1908) in Germany found that the guts of 100 specimens of *G. pulex* all contained plant remains, and that green algae, worms and insects were only occasionally present. In Germany, also, Willer (1922) found, in the guts of 196 specimens, mainly the tissues of higher plants; algae and animals occurred only occasionally. Wundsch (1922) in Germany and Mottram (1934) in England found, by experiment, that the shrimps preferred dead leaves to most other foods, but they did not offer animal foodstuffs. Margalef (1948*b*) in Spain found that the species fed exclusively on animals, chiefly insects and *Cyclops*.

Table 3. *The occurrence of animal and vegetable foodstuffs in the foreguts of specimens of* Gammarus duebeni *and* G. pulex *from Manx localities*

	No. examined	No. containing: Only vegetable matter	No. containing: Animal and vegetable matter	No. containing: Only animal matter
G. duebeni				
Specimens from five streams	50	37	13	0
Specimens from three rock pools	30	17	11	2
Specimens from two beaches	30	18	8	4
G. pulex				
Specimens from five streams	50	26	17	7

Dahl (1915) in Norway found that *Gammarus lacustris* feeds mainly on plant detritus, and that it often destroyed fish-nets. This has also been noted of *G. fasciatus* in North America (Clemens 1950). There would appear to be fairly general agreement that *Gammarus* feed largely on vegetable matter, and Sexton (1928) was able to maintain stocks of several species on a diet of dead elm leaves. Clemens (1950) also found this a satisfactory diet for *G. fasciatus*, although he also fed yeast and animal food to young and mature animals respectively, and Le Roux (1933) found that she obtained better results with *G. duebeni* when she fed them with chopped earthworm as well as leaves. During the present study *G. duebeni*, *G. pulex* and *G. z. zaddachi* were all successfully reared through two generations on elm leaves alone.

In order to compare the diet of *G. duebeni* and *G. pulex* in the Isle of Man the gut-contents of full-grown specimens from several localities were examined. Only the contents of the stomach and the extreme anterior end of the mid-gut were studied, and specimens with nothing in this part of the gut were rejected. The results are summarized in Table 3.

The vegetable matter, which was occasionally mixed with grit, was finely divided. Some of it was recognizably moss, but most was vascular plant tissue. Only three specimens of *G. duebeni* and one of *G. pulex* contained algae, and then only in minute quantities; the genera present were *Ulothrix*, *Navicula*, *Synedra* and *Pinnularia*. The animal matter consisted entirely of small fragments of arthropods. These were mostly too broken to identify, but in both species parts of Ephemeroptera and Plecoptera nymphs, Trichoptera larvae, chironomid larvae and *Gammarus* were recognized, and the remains of a *Jaera* were found in one specimen from a rock-pool. It is obvious that small soft-bodied animals, such as Protozoa, would escape detection, but careful search was made for the chaetae of annelids and none was found. Otherwise the only soft-bodied animals known to occur in any of the habitats were Platyhelminthes (*Procerodes ulvae* (Oer.) and *Polycelis cornuta* (Johnson)), Mollusca (*Littorina* spp., *Potamopyrgus jenkinsi* (Smith) and *Ancylastrum fluviatile* (Müller)) and occasional specimens of *Gordius*. These were all confined in dishes with large numbers of hungry *Gammarus* and only *Gordius* was seen to be eaten. Insects, oligochaetes and small *Gammarus* were frequently seen to be eaten in the laboratory, but *Asellus meridianus* Racovitza, which occurs in many Manx streams, was never attacked. It seems that oligochaetes, although readily eaten in the laboratory are not eaten in the field, probably because of their cryptic habits.

It can be seen from the table that the diet of *Gammarus duebeni* is similar in all three types of habitat investigated, and that animals form about one-quarter of the food. *G. pulex* also has a similar diet, although it would appear from the table that animals are more important to it. This difference is, however, probably not real, as the different samples differed considerably in this respect, and it would require much larger numbers of gut-examinations to reveal any consistent difference. It would seem, therefore, that the diet of both species is partly vegetable and partly animal, as was found also for *G. zaddachi* by Jones (1951), and for *G. fasciatus* by Clemens (1950), and that both species eat their own kind. The animals are apparently eaten while still alive or recently killed, as neither species will eat rotting animals in the laboratory. They will, however, feed readily on dead leaves, preferring the softer species, like elm and poplar, to harder ones like oak, hawthorn and beech; the last they will not eat at all. When given living plants, e.g. *Riccia*, *Fontinalis* and *Nasturtium*, they prefer, as noted by Wundsch and Mottram, dead leaves to living ones.

THE LIFE CYCLE

(*a*) *In the field*

Samples were collected at approximately monthly intervals from a stream and a beach. Most of the collections were made by Dr N. S. Jones. To obtain the samples the substratum was stirred up vigorously with the feet, and the resulting clouds of silt, vegetable debris, etc., were caught with a fine stramin hand-net, the contents of which were emptied at intervals into a dish. This process was repeated at various points until it was judged that at least 200 specimens had been obtained. The larger debris was then removed from the dish, and the rest transferred to a jar with formalin. In the laboratory the contents of the jar were further picked over and were poured on to

a sieve with meshes fine enough to retain the smallest specimens. They were then tipped into a saturated solution of calcium chloride, in which all the mineral particles and much of the plant debris sank, while all the *Gammarus* and nearly all the other animals floated. By repeatedly stirring the solution and pouring off the surface layer it was possible to retrieve every specimen of *Gammarus* in the sample. This is a modification of the technique proposed by Beak (1938). The *Gammarus* were stored in 90% alcohol containing 2% glycerol.

As the localities sampled were a small stony stream (Port Erin stream, Fig. 2, no. 9) and a stony beach at the mouth of a stream (Gansey beach, Fig. 2, no. 15), where the distribution of microhabitats was uniform, it is assumed that the samples were truly random samples of the population.

The specimens in each sample were then sorted into 1 mm. size-groups, and details of the sex and sex-condition of each specimen were recorded. The size-groups were 1–2, 3–4 mm., etc., measured from the base of the first antenna to the base of the telson, with the animal straightened out above a millimetre scale. In practice most specimens were not actually measured individually, but were matched against a series of specimens 1·5, 2·5 mm., etc., long. In this way it was possible comparatively rapidly to place most specimens shorter than 13 mm. long in their size-group. Larger specimens and those about which there was doubt were measured individually.

When examining the specimens for sex and sex-condition, females were classified as mature when the oostegites were fully developed and fringed by bristles. No specimens were found in which the oostegites were fully developed but without the fringe of bristles, although this phenomenon has been reported in *G. duebeni* by Legueux (1924) and Kinne (1952*a*), and in *G. pulex* by Heinze (1932), and is known also in other species. Specimens with developing oostegites were found in the 7–8 mm. size-group in samples from both localities, but not often in the smaller size-groups, and it was not found possible to determine the sex with certainty of all specimens below 8 mm. long. This is in agreement with the finding of Le Roux (1933) that the oostegites appear at 6–6·5 mm., but are difficult to see in such small specimens. The mature females were all between 8 and 14 mm. long in the samples from the stream, and 7–14 mm. long in the samples from the beach, but in both most were 9–12 mm. long. Females with oostegites which were not fully developed were found in all size-groups between 7 and 13 mm. long, and as this range greatly overlaps that of fully developed females it shows that some mature at smaller size than others.

It was not found possible morphologically to distinguish mature males from immature ones, as the development of sexual characters in this sex is continuous (Le Roux 1933). The sexual apertures were visible in only some male specimens in the 7–8 mm. size-group. In the samples from the stream four males were found which had small oostegites; in other respects these specimens were normal.

Figs. 5 and 6 and Table 4 give details of the monthly samples. The figures show the percentage of the total population in each size-group. Those below 8 mm. long have been centred, to indicate that sex was not determined, while in the larger size-groups the males are shown on the left and the females on the right. Mature females are shown cross-hatched. Only one mature female was found which was less than 8 mm. long, and she has been shown below the horizontal 8 mm. line (Fig. 5, April). From

Table 4. *Details of the random monthly samples from Gansey beach and Port Erin stream*

	Dates of sampling											
	23 Sept. 1949	22 Oct. 1949	24 Nov. and 23 Nov. 1949	30 Dec. 1949 and 3 Jan. 1950	28 Jan. 1950	27 Feb. 1950	18 Mar. 1950	12 Apr. 1950	12 May 1950	14 June 1950	12 July 1950	11 Aug. 1950
GANSEY BEACH												
No. of specimens	991	836	383	224	284	383	114	495	783	611	1620	1140
Mature females as % of total	0	0·1	0	3·1	6·0	56·1	55·3	26·7	13·5	4·7	1·4	0·2
Ovigerous females as % of mature females	—	100·0	—	75·0	64·7	86·9	87·2	93·3	78·2	72·5	36·4	50·0
% ovigerous females with young in pouch	—	100·0	—	11·1	9·1	6·4	10·9	9·8	16·7	4·8	0	0
No. of specimens in precopula	None	Very few	None	Some	Some	Many	Many	Many	Most	Many	Very few	Few
PORT ERIN STREAM												
No. of specimens	528	264	216	217	192	242	215	483	542	1875	1024	771
Mature females as % of total	6·6	6·8	20·8	27·6	28·2	25·6	29·3	23·6	12·2	4·6	1·4	2·2
Ovigerous females as % of mature females	94·4	94·6	86·7	96·7	92·6	92·0	84·2	98·4	94·0	68·7	57·1	76·5
% ovigerous females with young in pouch	18·2	17·6	0	1·7	8·0	14·0	5·7	8·1	14·5	20·4	25·0	7·7
No. of specimens in precopula	Several	Very few	Few	Some	Some	Many	Many	Many	Many	Few	Very few	Few

the figures and the table it can be seen that the life cycle in the two localities differed greatly. On the beach practically no mature females were found between August and November: in fact one was found in October, but this represents such a small percentage of the sample that it has not been possible to show it in the figure. From the end of December until February and March the number of mature females increased rapidly, and the table shows that most of these were breeding. Most of the young were produced in the period between late March and early May, after which there was a steady decline in breeding throughout the summer. It is possible by following the samples round the year to observe the growth of the new generation. In the stream mature females were present throughout the year, as were very small specimens, although there was apparently a slight decline in the production of young in the periods October to January and July to August. Most of the mature females were ovigerous, and young were present in the brood-pouches of some in nearly all months.

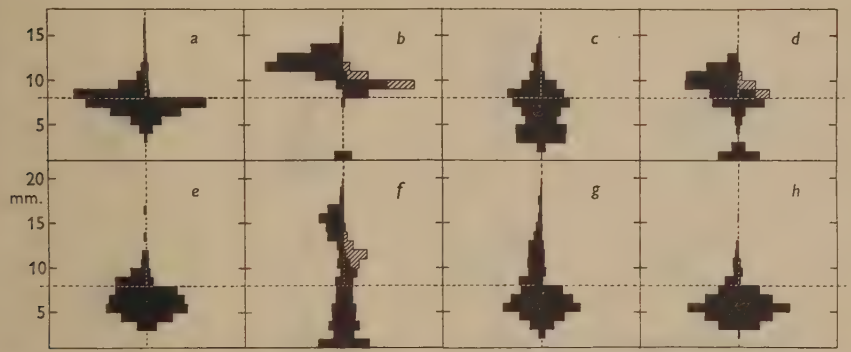

Fig. 7. Size and sex distribution in summer and winter samples of *G. duebeni* from beaches and rock-pools. Arranged as in Fig. 5. *a* and *b*, Gansey beach, 29 Aug. 1949 (1510 specimens) and 3 Jan. 1951 (171 specimens). *c* and *d*, Poyllvaaish beach (Fig. 2, no. 18), 28 July 1949 (1247 specimens) and 3 Jan. 1951 (866 specimens). *e* and *f*, rock-pools, Scarlet Point (Fig. 2, between nos. 18 and 19), 28 July 1949 (210 specimens) and 3 Jan. 1951 (945 specimens). *g*, rock-pool, Rant Gwyn, Caernarvonshire (23/236383), 20 July 1951 (1520 specimens). *h*, Rock-pool, Porth Solfach, Bardsey island 18 July 1951 (477 specimens).

To check if the life cycle found in these two habitats was typical of similar habitats elsewhere, similar samples taken in winter and late summer from other localities were analysed. Fig. 7 shows details of such samples from Poyllvaaish beach (Fig. 2, no. 18), a locality very similar to Gansey beach, and also two extra samples from the latter. It can be seen that the samples from Poyllvaaish are very similar to the corresponding samples from Gansey, and that the cycle at Gansey was similar in the different years. There are perhaps indications that breeding there began earlier in 1951 than in 1950, and that it began earlier at Poyllvaaish in 1951 than it did in Gansey. But apart from such minor differences the general cycle on the two beaches, and in different years on Gansey beach, seems to be much the same.

Fig. 7 also shows details of summer and winter samples from rock-pools in the Isle of Man, and of two summer samples from rock-pools in Wales. Here also it is clear that the cycle closely resembles that found on the beaches, although there are again

indications of slight differences in timing, e.g. breeding in the Manx rock-pools in January 1951 was slightly more advanced than it was on the nearby beaches.

Fig. 8 shows details of three winter and five summer samples from Manx streams and of summer samples from streams on the Lizard peninsula and Bardsey island. The Manx samples are broadly similar to those from Port Erin stream, and show no sign of cessation of breeding in late summer, although they do indicate that active breeding was occurring in some localities in January, which was apparently a slack period in Port Erin stream. It is clear also that in Cornwall too the stream population was actively breeding at a time when no breeding had been found in brackish water. The July sample from Bardsey island is of particular interest as it closely resembles the samples from brackish water. The water of this stream is fresh (Pyefinch 1937), but it is said to cease flowing every year. At the time the sample was taken there was no

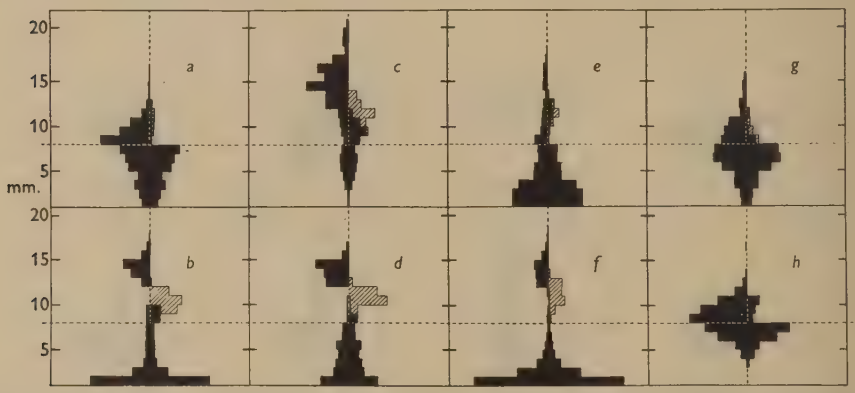

Fig. 8. Size and sex distribution in summer and winter samples of *G. duebeni* from freshwater streams. Arranged as in Fig. 5. *a* and *b*, Ballabeg stream (Fig. 2, no. 17 upper tributary), 29 July 1952 (2100 specimens) and 2 Jan. 1952 (465 specimens). *c*, Port Erin tributary (Fig. 2, no. 9) 29 Aug. 1949 (258 specimens). *d*, Ballagarmin stream (Fig. 2, no. 17 middle tributary), 2 Jan. 1951 (221 specimens). *e*, Rhenwyllan stream (Fig. 2, no. 14), 28 July 1952 (1366 specimens). *f*, Harbour Master's stream (Fig. 2, no. 10), 31 Dec. 1950 (865 specimens). *g*, Poltesco river, Cornwall (Fig. 3, no. 14), 22 Aug. 1952 (434 specimens). *h*, Bau y Rhigol stream, Bardsey island, 18 July 1951 (323 specimens).

flow, and the *Gammarus* were confined to a series of pools in the bed both near its mouth and at its source at 200 ft. It would seem, therefore, that the type of life cycle is controlled not by the salinity of the water, but by current or some other factor associated with a running stream but not with rock-pools, beaches or pools in the bed of a stream.

Comparison of the life cycle found in brackish water in the Isle of Man with that found at Kiel by Kinne (1952*a*) is of considerable interest. Our investigations were made without mutual knowledge, and it is fortunate that we adopted similar methods. Kinne did not seriously attempt to assess the numbers of specimens below 4 mm. long, and in illustrating his results he appears to have smoothed his figures. He also did not distinguish between mature and immature females when presenting his results, because from July to January he found many females with fully developed oostegites but without bristles, and he could not be sure if these had already bred once before

entering upon a resting period. Apart, however, from these small differences our results are strictly comparable. They give an almost identical picture, but there are two important differences. First, the sex-ratio on Gansey beach was not heavily weighted in favour of the females in most months as at Kiel; in most months the males preponderated, but this was almost certainly because many of the undetermined smaller specimens were females. In the February, March, April and May samples it was possible to determine the true sex-ratio of females to males, which was 2·4, 1·5, 1·1 and 0·9 respectively. This indicates first that there was a real preponderance of females, and secondly that once breeding started they died off more rapidly than the males. This last point is clear also from the persistence of large males in the samples until October, two months after the last mature females were found. Kinne explains

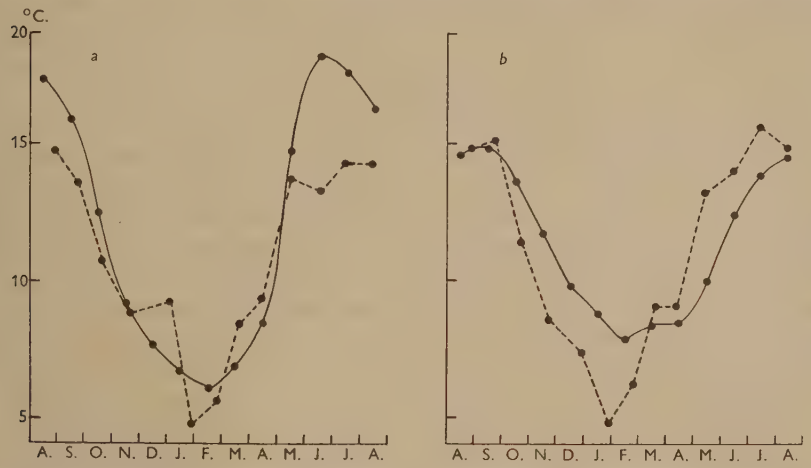

Fig. 9. Temperatures of streams, sea and air, 1949–50. *a*, broken line, Port Erin stream; whole line, mean air temperature. *b*, broken line, Rushen stream, top of Gansey beach; whole line, mean sea temperature.

his variation in sex-ratio on his results showing that temperature of egg-ripening controls sex, low temperatures producing males and high ones females. It seems possible that this applies also in the Isle of Man, although it is clear that there the critical temperature must be higher than Kinne's 5–6° C. because the temperature at Gansey beach hardly fell below this (Fig. 9). Kinne (1952*b*) has, however, himself suggested that this critical temperature may vary with the temperature to which the shrimps are adapted.

A second point of difference was the total absence from all the British samples of females with fully developed oostegites but without the fringe of hairs. These Kinne showed to be females which had stopped breeding, and Le Roux (1933) produced the same effect by sterilizing females with radium. I suggest that its absence in the British localities was because of their lower summer temperatures. Gansey beach and the other British localities studied in the late summer all had water temperatures below 16° C., whereas in the Kleiner Kiel the temperature rose to 16° C. in May or June and later to well above 20° C. Kinne shows that in his population some of the young females reached a length of about 14 mm. by the end of May, so some of them were

able to start breeding before being inhibited in some way in the autumn. On Gansey beach the young females grew much more slowly, probably because of lower temperatures, and none was big enough to breed before July or August when the 'close season' (Rühezeit of Kinne) had already set in.

Fig. 9 shows the mean monthly air and sea temperatures at Port Erin (data kindly supplied by Dr N. S. Jones from the records of the Marine Biological Station), and also the water temperatures in Port Erin stream and at the top of Gansey beach when the samples were collected. The temperatures of the two streams were almost the same and so do not appear to account for the differences in breeding cycle between the two localities. On the beach the *Gammarus* were often covered by sea water, the temperature of which has therefore been shown, but nothing in the sea and stream temperature curves, nor in the relation between them, seems to be correlated with the peculiar life cycle found on the beach. Also sea temperature can have had no direct influence on the rock-pool populations, which were all situated at or above high spring-tide level. It was, however, observed both by Dr Jones and myself that on the beach in July, August and September the *Gammarus* were mostly to be found at and for a few yards below high-water springs in the main current of the stream, whereas at other times of year they were lower down the beach, generally distributed over the fan-shaped area of *Enteromorpha*-covered stones through which the stream water flowed. This indicated that in late summer and autumn there might be a temperature difference between the top of the beach, where the records were made, and the area only a few yards below, where most of the specimens were, and that the shrimps were seeking a temperature as low as possible without actually leaving the brackish water. This was confirmed by observations made at low tide on 30 July 1952, a hot day (shade temp. 26° C. at midday) after a long drought. At 9.30 G.M.T. the temperature of the stream at and above high water springs was 13·7° C. and remained so until 11.45 when observations ceased. At high neap-tide level, the lower limit of *G. duebeni* except for stray specimens, the temperature rose from 14·5° C. at 9.30 to 17·4° C. at 11.45, and at mid-tide level, well below the lower limit of the species, it rose from 16·5 to 19·5° C. There was therefore by midday a steep temperature gradient from 13·7 to 19·5° C. over a distance of about 200 m. Although the shrimps can stand much higher temperatures than this, they may move along a short steep temperature gradient on beaches in search of their optimum. They cannot, however, escape completely from the higher temperatures without becoming densely crowded or entering fresh water, and this they never seem to do on Gansey beach. It would appear therefore that, at least for some part of most days in late summer and autumn, the shrimps on beaches are subjected to temperatures one, two or possibly more degrees higher than those in streams. The same must also apply to rock-pools which become very warm in hot weather. It seems very probable that the close season found in brackish water is an indirect result of these high temperatures.

It should perhaps be stressed here that the close season on Gansey beach is somewhat different in character from that studied by Kinne, although occurring at the same time of year. In his population, young females started to breed and then stopped for a while, probably because of falling temperature (Kinne 1953). In the British brackish localities the older females died during the summer, and the largest of the

young ones had barely reached adult size by September, when the temperature began to fall. Presumably this temperature fall prevented their starting to breed, and it may be that the difference between the life cycles in brackish and fresh water is because this fall was less steep in the latter. Possibly higher temperatures in brackish waters cause the old females to die sooner, but are not high enough to allow the young to mature before the autumn drop, while the lower stream temperatures permit old breeding females to persist, and the less steep temperature drop in the stream does not prevent the next generation from breeding before the old ones have gone. This explanation accounts both for the differences between the life cycles found in Britain and Germany and those found in British fresh and brackish water. Also it is not incompatible with the fact that breeding can be obtained in the laboratory at temperatures as high as 20° C., which would be difficult to reconcile with any suggestion that high temperature as such interfered with breeding.

(*b*) *Lengths of the various stages*

In the course of breeding experiments, described below, various individuals and batches of shrimps were kept in small covered glass or enamel dishes in 20% sea water, and fed on elm leaves. They were examined at frequent intervals and the following data were collected.

Precopula, which has been described in this species by Le Roux (1933) lasts for 2 days to several weeks. The duration is possibly more or less related to temperature as well as to the female's nearness to moulting at the time it begins, but no observations on this were made. Both in the laboratory and in the field, immature females were frequently observed in precopula, but these were all in their last immature instar.

The time taken for the eggs to hatch in the brood-pouch varied with temperature as follows:

Mean temperature (° C.)	...	18	15·5	15	12·5	4·7
Incubation period (days)	...	14	18	21	22–27	54–59

These figures are in general agreement with those of Forsman (1951). Once hatched, the young remained for some days (up to 5 at 12·5° C.) in the brood-pouch, leaving one by one, and they were often observed to feed on detritus swept in by their mother's respiratory current.

In the laboratory the time taken to reach sexual maturity varied from 23 to 30 weeks (mean temp. 15–20° C.), and the sexes matured together. This applied to specimens of both fresh and brackish water origin. This period is rather longer than that recorded by Le Roux, but her specimens were fed on earthworm as well as leaves. In four dishes, however, which all contained young of brackish water origin, 45–48 weeks passed before any mature specimens appeared. It is thought that this slow development was because the specimens in these particular dishes were very crowded, each having an area of only about 10 sq. cm. It may be noted though that in the field they have been found more crowded than this; for instance, 1520 specimens were collected from a rock-pool in N. Wales of which the area was only about 1 m.^{2}. Many specimens both of fresh and brackish water origin lived for at least 20 months and bred several times, and one male from brackish water stock lived for nearly 25 months. The oldest female recorded lived for only 15 months.

As has been observed in other species, and particularly in *G. duebeni* (Sexton 1924), the males tend to eat the females instead of fertilizing them when they moult. This has been observed both in the laboratory and in the field, and it was usually found that those which lived longest in any batch of specimens were males. Both sexes, but more particularly the males, chase and eat the young; this is in marked contrast with their reaction to the females, of whose presence and readiness to mate they only seem to be aware when they touch them with their antennae.

The monthly samples from Port Erin stream and Gansey beach also give some information about the time taken to reach maturity and the length of life. On the beach (Fig. 5) the new generation began to appear in early April, and the first mature females were found at the end of December. This shows that approximately 37 weeks were needed to reach maturity. Similarly, the last of the old male specimens were found in October, and the last of the mature females were found in July. This indicates a maximum life-span of about 18 months for males and 15 for females. In the stream (Fig. 6) the position was less clear because of the more or less continuous breeding, but it can be seen that heavy breeding occurred from April to June, and that the young produced then can be followed through to the August sample. If one assumes that the same heavy breeding occurred in the spring of 1949 as in 1950 it should be possible to trace this generation in the September and October samples. Unfortunately, heavy production of young in September introduced complications, but in the October sample a small peak is visible in the 7–8 mm. size-group, which may represent the spring hatch. Also in the November and early January samples there is a marked increase in the relative numbers of mature females, and this probably represents maturation of this hatch. If this is so specimens born about mid-May take about 31 weeks to become mature about mid-December. Similarly, the last large males of this hatch can be traced through to the August sample, and, again assuming that 1949 was like 1950, a few are present in the September sample. This indicates a maximum life-span of about 17 months for males, and in the same way one can arrive at a figure of about 15 months for females.

There is therefore general agreement between the two localities, and, when account is taken of the differences in temperature, with the laboratory observations also. Two points of disagreement are, however, of interest. First, despite the higher temperature, some laboratory specimens lived for over 20 months. Probably this is merely the result of their sheltered and well-fed existence. Secondly, although the agreement between the time taken to reach maturity on the beach and in the stream is fairly close it does appear that this stage in the life cycle took longer on the beach. These data are admittedly very approximate, but it may be significant that the species was far more abundant on the beach, and that there is reason to believe that crowding retards development.

FACTORS CONTROLLING LOCAL DISTRIBUTION

G. duebeni was absent from many streams on the Isle of Man and the Lizard peninsula, which were apparently suitable as regards substratum, current speed, shelter and food supply, and were without obvious physical barriers, such as falls, which would prevent immigration from the coast. In the Isle of Man the species was either present in, or

absent from, the various streams, but on the Lizard peninsula, in Mawgan creek (Fig. 3, no. 25), it was common for only about 250 m. from the mouth of the stream, to a height of about 8 m. O.D. and quite absent upstream. Similar restricted distributions have been observed by Beadle & Cragg (1940*b*) in the Inner Hebrides and by Prof. Cragg on Anglesey (see above).

It seemed probable that the absence of the species from some streams would be explained by physical or chemical factors in the environment, or by associated fauna, and several such possible controlling factors were studied. The results of these investigations were entirely negative, but they serve to show that some factors, which might be expected to control the distribution of the species, do not, in fact, do so, and they also throw some doubt on the validity of some ideas that have been advanced concerning the detailed distribution of *G. pulex*.

(*a*) *Geology of drainage basins*

The geology of the Isle of Man has been described by Lamplugh (1903). The northern quarter of the island consists of glacial drifts and morainic material, and most of the rest, of hard Palaeozoic slates with igneous intrusions. In the south-east is an area of Carboniferous limestone across which flow several of the streams in which *G. duebeni* was found. As, however, *G. duebeni* (and *G. pulex*), occurs also in streams, both to the north-east and to the south-west of the limestone area, which drain only slate, it seems clear that gross geological structure does not explain its distribution.

Similarly, no correlation between geology and shrimp distribution could be found on the Lizard. The southern part of the peninsula consists of serpentine, and all the streams in which *G. duebeni* was found drain this rock; but so do at least two streams in which the species was not found. North of the serpentine the country consists of horneblende schists and gabbros, which, chemically, are not greatly dissimilar from serpentine, and on which *G. duebeni* was not found. The northern third of the peninsula is sandstone, and it was on this rock that *G. duebeni* was found penetrating for only about 250 m. into fresh water.

Finally, in Ireland also, the occurrence of *G. duebeni* cannot be correlated with gross geological structure. Much of the country is limestone, but there are areas of igneous rock and hard Precambrian schists. On one area of igneous rock, the Wicklow mountains, the species appears to be absent, but on others, e.g. Co. Antrim, it occurs. It also occurs widely on igneous and Precambrian rocks in West Donegal.

(*b*) *Dissolved salts*

(1) The Isle of Man. It was at first thought that the salinity of the water would prove to be important, and during the initial survey, made during dry weather on 20–28 July 1949, the chloride content of many stream waters was determined by titration with silver nitrate, and the titration alkalinity and pH were also measured, the latter by means of indicators and a set of standard buffered solutions: none of these factors could be correlated with the occurrence of *Gammarus*. Table 5 shows that the ranges found in streams with and without *Gammarus* overlapped considerably. Results from streams which for some physical reason did not appear to be suitable for *Gammarus* are not included in this table.

It may be noted here that *G. duebeni* has been recorded from very acid waters (pH as low as 4·8) in Ireland (Reid 1939); it would appear therefore that this species can, like many Entomostraca (Lowndes 1952) tolerate a wide range of pH.

Table 5. *The ranges of* pH, *titration alkalinity, and chloride found in 49 streams in all parts of the Isle of Man, 20–28 July 1949*

(Only those streams in which shrimps occurred or which appeared suitable for them are included in the table.)

Localities containing:	No. of localities	pH	CO_3 (mg./l.)	Cl (mg./l.)
G. duebeni	12	7·1–8·2	13–137	29–98
G. pulex	6	6·8–8·0	8–60	21–51
No *Gammarus*	31	5·9–7·7	2–78	16–58

Further samples were taken during the first half of April 1950, and on these were determined specific conductivity, alkalinity, chloride, sulphate, calcium and magnesium. Chemical methods employed were those of Thresh, Beale & Suckling (1949), and conductivity was measured with a Mullard meter. The results are shown in Table 6, from which it is apparent that no correlation was found between any of the factors analysed and the occurrence of shrimps.

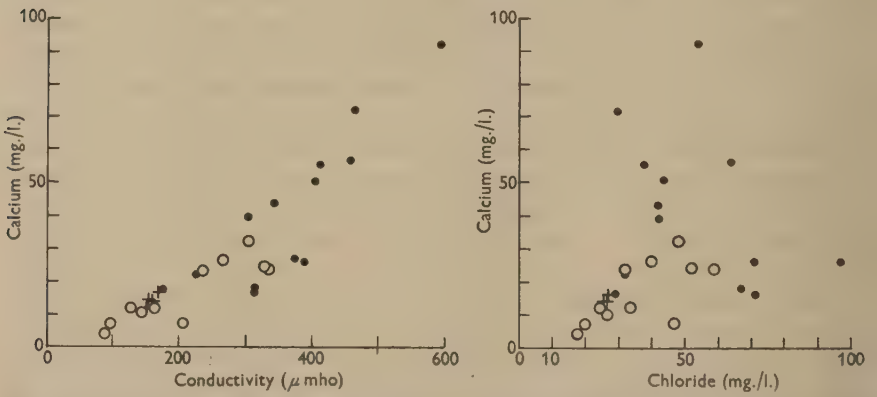

Fig. 10. Calcium and conductivity and calcium and chloride plotted against one another in samples from Manx streams collected in Apr. 1950. The streams shown as crosses contained *G. pulex*, as dots *G. duebeni* and as circles no *Gammarus*.

As calcium is well known to influence osmoregulation (Krogh 1939), and as *G. duebeni* is normally a brackish water species, the ratios of calcium to chloride and calcium to conductivity, which affords some measurement of total ions, were investigated. These are shown graphically in Fig. 10, which indicates that while, on the whole, *G. duebeni* was found in the harder and more saline waters, there were waters as hard and as saline which contained none.

Several of the localities sampled in April had also been sampled during the previous July, when only alkalinity and chloride had been measured. The results of the two series of analyses differed somewhat (Table 6), and, when they were plotted against

Table 6. *Details of water analyses and occurrences of* Gammarus *in Manx streams, July 1949 and April 1950*

(The stream numbers are those shown in Fig. 2. For each locality the approximate distance of the sampling point from the sea is shown.)

Stream no.	Locality	Species present	Approx. distance from sea (m.)	April 1950						July 1949	
				Conductivity (μmho)	Cl^- (mg./l.)	$CO_3^=$ (mg./l.)	$SO_4^=$ (mg./l.)	Ca^{++} (mg./l.)	Mg^{++} (mg./l.)	Cl^- (mg./l.)	CO_3^{++} (mg./l.)
2	River Neb	None	2000	88	18	2	tr.	4	< 3·0	20	13
7	Fleshwick stream	None	400	204	47	4	< 11	7	< 3·0	59	15
8	Spaldrick stream	*duebeni*	100	313	67	7	14	18	5·0	59	36
9	Atholl Glen, Port Erin	*duebeni*	200	458	64	39	17	56	5·2	52	56
	Port Erin tributary	*duebeni*	200	374	71	16	15	26	3·4	51	40
10	Harbour Master's stream	*duebeni*	100	389	97	15	14	25	5·6	69	31
11	Sound stream	*duebeni*	700	313	71	10	15	16	5·5	98	60
13	Glenchass	None	300	328	59	17	15	24	3·6	—	—
15	Rushen stream	None	1000	336	52	20	16	24	3·1	52	78
16	Colby river	None	1300	173	34	7	< 11	12	5·1	31	7
	Colby tributary	None	1300	267	40	12	15	26	5·5	35	20
17	Arbory stream, near mouth	*duebeni*	100	405	44	54	14	50	5·5	49	60
	Ballagarmin tributary	*duebeni*	1600	304	42	32	15	39	< 3·0	—	—
	Ballabeg tributary	*duebeni*	2200	346	42	58	15	43	4·7	36	51
	Arbory tributary	None	2400	302	48	27	16	32	4·0	—	—
	Arbory stream, Arbory	None	2300	234	32	19	12	23	4·8	31	19
18	Poyllvaaish stream	*duebeni*	50	595	54	113	13	92	6·9	53	137
19	Silverburn below tribs.	*pulex**	2300	156	26	13	< 11	14	3·3	27	18
	Ballasalla stream	*duebeni*	2300	412	38	64	11	55	5·5	—	—
	St Marks tributary	*pulex*	2800	170	27	12	< 11	16	3·7	—	—
	Silverburn above tribs.	*pulex*	2800	150	26	10	< 11	11	< 3·0	25	5
20	Ronaldsway stream	*duebeni*	1300	465	30	91	18	71	7·8	—	—
21	Santon burn	None	2000	128	25	8	< 11	12	3·3	23	10
	Ballalona stream	*duebeni*	2000	227	32	18	11·3	22	4·1	36	30
22	Glen Grenaugh (upper)	*duebeni*	1200	176	29	13	< 11	16	3·5	30	13
23	Upper Crogga river	None	2300	145	27	8	12	10	3·2	28	9
24	River Dhoo	*pulex*	1900	158	26	14	< 11	14	< 3·0	26	14
	River Glass	None	1500	99	20	4	< 11	7	< 3·0	18	9

* A few *duebeni* also present (see text).

one another, two interesting points emerged (Fig. 11). First, the alkalinity differed quite irregularly between the two sets of samples, although it tended to be higher in July than in April, possibly because of photosynthesis. It is therefore certainly of little value for assessing gross chemical differences between stream waters. Secondly, the chloride content of the more inland localities was found to be very much the same in April as in July, despite a considerable difference in water-level. In localities near the

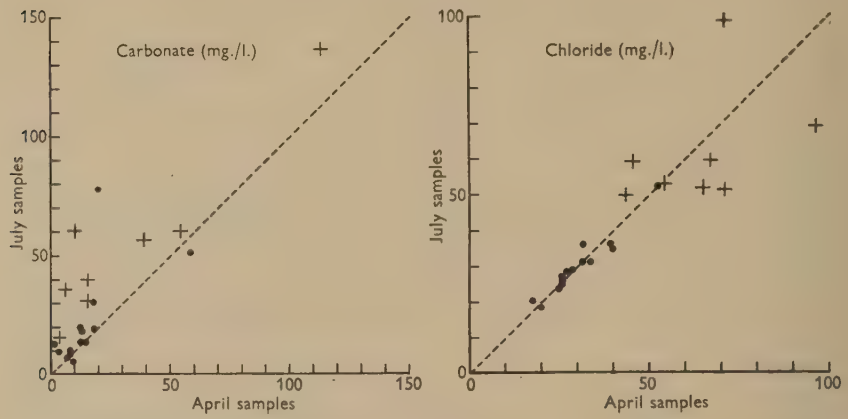

Fig. 11. Values of carbonate and chloride determined in Manx streams in samples taken in July 1949 and April 1950. Each set of analyses is plotted against the other. Sampling points more than 1 km. from the sea are shown as dots those less than 700 m. from the sea as crosses. The dotted lines are where the points would fall if both sets of analyses had given the same results.

sea, however, the chloride content was much more variable, as well as being generally greater. This indicates that at least some of the chloride, and therefore of other ions also, in these streams near the sea, is normally derived from sea spray, and that the variation is caused by the prevalence of storms, direction of spray drift, etc. It follows therefore that all the streams near the sea normally receive ions from sea water, and that if any of these are important for *G. duebeni* they are available there at least in small amounts.

Thienemann (1912) found that *G. pulex* was larger in hard than in soft waters, and several authors (e.g. Wundsch 1922, Titcomb 1927) have suggested that water-hardness is a limiting factor in the ecology of freshwater *Gammarus*. Schumann (1928) suggested that the occurrence of some species is influenced by the balance of certain ions, and that the minimum amount of calcium necessary is 13 mg. $CaCO_3$ per litre (= 5·2 mg. Ca), some of which must be present as bicarbonate. As all the Manx streams investigated contained more calcium than this, and there was no reason to suppose that it was present in any other form than the usual $CaCO_3/Ca(HCO_3)_2$ complex, it would appear that calcium is not there a limiting factor. Schumann suggests that the ratios Ca/Mg and Ca + Mg/Na show differences between streams with and without *Gammarus*, being higher in the former. He made no analyses of sodium, but calculated it on the assumption that all the chloride was present

as NaCl. This has been done for the Manx streams and the ranges of these ratios were:

Ca/Mg	Localities with *G. duebeni*	2·9–13·3
	Localities with *G. pulex*	*c.* 4·0–*c.* 4·6
	Localities without *Gammarus*	*c.* 1·3–7·7
Ca+Mg/calculated Na	Localities with *G. duebeni*	0·47–2·80
	Localities with *G. pulex*	0·67–1·12
	Localities without *Gammarus*	0·53–1·31

These ranges overlap considerably, and do not indicate that ion-imbalance controls the occurrence of *G. duebeni* in the Isle of Man.

Schumann's method of estimating the sodium content of the water is probably very unreliable, and as sodium, potassium, calcium, magnesium, chloride and sulphate are the ions in the content of which sea water most differs from fresh water, these were determined on a further series of samples taken from Manx streams in April 1952. Chloride, sulphate and conductivity were determined as before, calcium and magnesium by direct titration with disodium versenate (Betz & Noll 1950), and sodium and potassium with a flame-photometer. Reducible iron was also qualitatively investigated with α-α′-dipyridyl. The results are shown in Table 7. As before, no single ion, nor the ratios conductivity/Ca, Ca/Cl, Ca/Mg and Ca+Mg/Na showed any correlation with the occurrence of *Gammarus*.

Some of the streams sampled in April 1952 were the same as those sampled in April 1950, and comparison between Tables 6 and 7 shows that the amounts of the various ions found at the two times of sampling were of much the same order. The only exceptions to this were magnesium, which was everywhere higher in 1952, and sulphate which in a few streams was much higher. It seems probable that the magnesium determinations made in 1950 were less reliable than those made, by the simpler technique, in 1952. The increase in the sulphate of some streams remains unexplained, but it may have been due to fertilizers.

It seems, therefore, that none of the ions analysed nor total salt content, as shown by conductivity, is a controlling factor in the distribution of *G. duebeni* in the Isle of Man. Also in view of the presence of sea spray in streams near the coast, from many of which *G. duebeni* is absent, it is unlikely that any trace element or organic substance normally present in seawater can exert a controlling influence. Support is also lent to this suggestion by the fact that the species will live, grow and reproduce in brackish water made from analytically pure salts (see below).

(2) The Lizard Peninsula. Between 21 and 23 August 1952 water samples were collected from several streams on the Lizard peninsula, and analyses were made by the methods used on the Manx samples earlier in the year. Details of the analyses are shown in Table 8. As in the Isle of Man no correlation was found between the amount of any of the ions present in the water, nor any combination between them, and the occurrence of *G. duebeni*. At first sight it appeared that magnesium might be a factor of importance as many of the streams on the peninsula are rich in this ion, and almost all the streams where *G. duebeni* was found contained more magnesium than did those from which it was absent. As, however, the Manx samples had already shown that the species can thrive in waters much less rich in this ion it cannot by itself be a controlling factor.

Table 7. *Details of water analyses and occurrence of* Gammarus *in Manx streams April 1952*

Stream no. (Fig. 2)	Locality	Species present	Conductivity (μmho)	Cl^- (mg./l.)	CO_3^- (mg./l.)	SO_4^- (mg./l.)	Ca^{++} (mg./l.)	Mg^{++} (mg./l.)	Na^+ (mg./l.)	K^+ (mg./l.)	Fe^{++}
7	Fleshwick stream	None	204	49	9	10	9	6·2	27	4·7	+
8	Spaldrick stream	*duebeni*	285	64	31	27	25	5·7	31	14·4	+
9	Atholl Glen, Port Erin	*duebeni*	454	64	112	38	68	14·8	37	11·0	0
	Port Erin tributary	*duebeni*	328	75	28	30	27	9·3	35	7·3	0
10	Harbour Master's stream	*duebeni*	344	79	49	25	35	11·0	43	6·5	+
15	Gansey stream	None	301	54	57	—	51	10·2	50	11·6	+
17	Lower tributary	*duebeni*	530	47	262	41	116	15·8	26	13·5	+
	Ballagarmin tributary	*duebeni*	274	41	72	15	43	9·4	23	9·5	+
	Ballabeg tributary	*duebeni*	307	40	106	9	48	12·0	22	11·0	++*
	Arbory stream, Arbory	None	240	34	52	12	32	9·6	20	6·5	+
19	Silverburn below tribs.	*pulex*	163	27	25	7	15	4·4	14	4·0	+
	Ballasalla stream	*duebeni*	356	41	142	27	44	21·8	21	6·5	0
22	Glen Grenaugh (lower)	*duebeni*	312	49	73	12	29	6·8	29	6·5	+
	Lower tributary	*duebeni*	243	36	52	10	27	16·3	19	7·3	0
23	Lower tributary	*pulex*	243	41	30	41	21	9·2	24	6·5	0
	Upper tributary	*duebeni*	248	41	48	9	22	10·6	23	4·7	0
	Crogga river above tribs.	None	183	32	25	13	14	8·1	15	4·4	0

* ++ represents $< 0{\cdot}5$ mg./l. of reducible iron as determined with α-α'-dipyridyl.

Table 8. *Details of water analysis and occurrence of* Gammarus *in streams on the Lizard peninsula, August 1952*

Stream no. (Fig. 3)	Locality	Species present	Conductivity (μmho)	Cl^- (mg./l.)	$SO_4^=$ (mg./l.)	Ca^{++} (mg./l.)	Mg^{++} (mg./l.)	Na^+ (mg./l.)	K^+ (mg./l.)
3	Goonhusband	*pulex*	340	60	22	56	12	20	3·1
4	Tangies	None	381	76	14	27	11	37	13·3
5	Gweoleath	*pulex*	535	60	17	51	33	28	2·5
6	Chypons	None	489	73	23	34	39	30	2·1
7	Polurrian	None	755	110	25	104	75	68	2·3
8	Trenance	*duebeni*	465	92	20	60	83	46	3·2
11	Crochall	*duebeni*	519	104	32	18	87	42	0·9
12	Lizard Downs	*duebeni*	725	209	26	19	68	83	1·3
13	St Ruan	*duebeni*	617	102	18	29	69	48	2·3
14	Poltesco, Trerise	None	438	75	21	17	51	32	1·6
	Poltesco trib. Crowgey	*duebeni*	580	94	21	25	79	45	2·4
15	Kennack	*duebeni*	504	91	20	32	60	44	3·9
18	Coverack	None	595	89	26	78	39	53	2·5
20	Mill Mehal	None	340	54	14	31	23	21	3·2
24	Caeryallack	None	264	44	14	27	17	16	3·2
25	Mawgan creek	None*	317	67	14	36	16	23	5·1
29	Gweek creek	None	169	39	tr.	12	6·3	13	2·7
31	Nancenoy	None	229	46	17	20	11	15	3·6

* *G. duebeni* was present in this water for about 250 m. above the upper limit of the tide.

(3) Anglesey. In January 1950 water samples were collected from many streams on Anglesey, Holy Island and the nearby mainland. Prof. Cragg also made a number of analyses of waters from this area in 1938–39, which he has kindly allowed me to quote. A summary of these analyses is given in Table 9.

Table 9. *The ranges of* pH, *conductivity, chloride, calcium and magnesium found in streams in Anglesey, Holy Island and the nearby mainland by the author in January 1950 and by Prof. J. B. Cragg in 1938–39*

(Only those streams in which *Gammarus* occurred or which appeared suitable for them were included in the table. The Holy Island localities are shown separately from the others.)

	No. of localities	pH	Conductivity (μmho)	Cl^- (mg./l.)	Ca^{++} (mg./l.)	Mg^{++} (mg./l.)
January 1950						
Containing *G. pulex*	36	6·8–8·2	52–542	11–57	3–91	< 3·0–9·0
Containing *G. duebeni* (Holy I.)	2	7·5–7·6	565–756	122–158	48–67	6·1–7·9
Containing no *Gammarus*	16	6·8–8·2	168–435	26–62	12–89	< 3·0–9·4
Containing no *Gammarus* (Holy I.)	1	7·5	725	115	47	9·1
1938–39 (J. B. Cragg)						
Containing *G. pulex*	12	7·9–8·2	—	—	3–140	3–10
Containing *G. duebeni* (Holy I.)	3*	7·6–7·8	—	—	35–51	6–10

* One of these localities was sampled four times.

As already stated *G. duebeni* was only found to be fully established in fresh water on Holy Island, and the streams there were clearly rather saline. These analyses therefore give no indication as to the reason for the absence of the species from Anglesey itself, but they are of some interest when applied to the distribution of *G. pulex*. This species was apparently absent from many streams on the main island which appeared to be physiographically suitable. In fact, all of those studied contained the type of microhabitat in which one expects to find the species. According to Schumann (1928) it is impossible for this species to harden its cuticle after moulting unless more than 5·2 mg. Ca/l. is present in solution. Calcium would appear therefore to be a very likely controlling factor, but both Prof. Cragg and I found the species in waters containing less than 5 mg. Ca/l., and the specimens I obtained were quite normal. These records refer to the easterly streams shown on the Welsh mainland in Fig. 4, and although Prof. Cragg and I took our samples in different seasons of different years our analysis figures agree closely. It may also be noted here that *G. pulex* is abundant in Llyn Tegid, Merionethshire, where the water contains less than 4 mg. Ca/l.

Schumann also suggested that the ratios Ca/Mg and Ca+Mg/calculated Na are important for *G. pulex* (see above, p. 68). In the analyses of water samples from Anglesey and the nearby mainland these ratios were:

Ca/Mg	Localities with *G. pulex*	2·0–16·6
	Localities without *Gammarus*	1·6–12·9
Ca+Mg/calculated Na	Localities with *G. pulex*	0·70–4·97
	Localities without *Gammarus*	0·71–4·23

It is therefore clear that Schumann's ideas about the importance of these ions to *G. pulex* are erroneous, as they have already been shown to be for *G. duebeni* in the Isle of Man, and that no chemical explanation has so far been advanced that will account for the detailed distribution of these species.

(*c*) *Temperature*

As already stated, the temperatures of two streams in the Isle of Man in one of which *G. duebeni* was abundant, while in the other no *Gammarus* occurred above high-tide level were recorded every month for 13 months. Fig. 9 shows that the temperatures in the two streams were at all times very similar. It is clear therefore that the absence of the species from one of them was not caused by its temperature, and this presumably applies to other Manx streams also, as the island is small, and the streams are all similar in general appearance, and without exception fed by run-off water from hard rock. The same general remarks apply also to the streams on the Lizard peninsula.

(*d*) *Associated fauna*

Pentland (1930) suggested that chemical composition of the water does not control the distribution of *Gammarus* spp. in North American fresh waters, but that temperature, vegetation and the presence of enemies may be factors of importance. Water chemistry and temperature have already been discussed, and, in order to see if any correlation between flora and fauna and the occurrence of *Gammarus* could be found, seventeen Manx streams were investigated. All these streams were small (1–2 m. wide) and fairly swiftly flowing over stony or rocky substrata, and all contained considerable amounts of dead leaves, sticks, etc., from trees along their banks. Nine of them contained large populations of *G. duebeni* and eight were without *Gammarus*. The streams and their numbers as shown on Fig. 2 were as follows:

Streams containing *G. duebeni*		
Spaldrick stream	8	
Port Erin stream	9	
Port Erin tributary	9	
Harbour Master's stream	10	
Sound stream	11	
Ballagarmin stream	17	lower right-bank tributary
Ballabeg stream	17	lower left-bank tributary
Glen Grenaugh	22	
Crogga river, upper tributary	23	
Streams without *Gammarus*		
Croggenmooar stream	6	
Croggenmooar, lower tributary	6	
Fleshwick stream	7	
Glenchass stream	13	
Rushen stream	15	
Arbory stream, upper reaches	17	
Crogga river, upper reaches	23	
Bishop's Glen	North of area shown on Fig. 2	

The microscopic flora was not investigated and was not abundant in any of the streams. *Fontinalis*, *Nasturtium officinale* R.Br. and *Apium* sp. occurred sparsely in some streams of both groups, but two streams in each group were without macroscopic vegetation. Some *Hypnum* sp. occurred in two streams without *Gammarus*.

The following animals were found in some of both groups of streams:

Planaria alpina Dana
Polycelis cornuta (Johnson)
Gordius sp.
Oligochaeta
Pisidium sp.
Limnaea pereger (Müller)
L. truncatula (Müller)
Ancylastrum fluviatile (Müller)
Asellus meridianus Racovitza
Baëtis rhodani (Pictet)
Baëtis sp.
Rhithrogena semicolorata (Curtis)
Nemoura cinerea Retz.
Protonemura meyeri (Pict.)
Amphinemura sulcicollis Steph.
Leuctra hippopus Kempny
L. fusca L.
Chloroperla spp.
Agapetus sp.
Rhyacophila sp.
Plectrocnemia sp.
Hydropsyche sp.
Philopotamus montanus (Donovan)
Odontocerum albicorne (Scopoli)
Stenophylax sp.
Hydraena sp.
Helmidae
Helodes sp.
Tipula sp.
Pedicia sp.
Dicranota sp.
Simulium spp.
Orthocladiinae
Tanypodinae
Chironominae
Salmo trutta L.

The last species, which would appear to be the most formidable carnivore in the fauna, was common in one stream containing *Gammarus* and present in two others; it was common in three streams without *Gammarus* and probably present in two others. It is difficult to be certain that the presence of trout was always detected, but in some of the streams of both groups they were certainly uncommon, if not altogether absent.

The following animals were found in one *Gammarus* stream only and not in any stream without *Gammarus*: *Glossiphonia complanata* (L.), *Potamopyrgus jenkinsi*, *Pericoma* sp. and Stratyomyidae, and present in one or two streams without *Gammarus* but not found together with it were: Ostracoda, *Diura bicaudata* (L.), Dytiscidae, *Heptagenia* sp. and *Anabolia* sp. Of these animals *Potamopyrgus jenkinsi* was the only one which was at all common, but as it occurred in only one stream, and as this seems to be the only locality in which it occurs on the island, from which it has not previously been recorded, it cannot affect the distribution of *Gammarus*. Of the others Ostracoda may have been overlooked elsewhere, and it is difficult to see how they can markedly influence *Gammarus*; and of the two carnivores the Dytiscid larvae were scarce and only one specimen of *Diura bicaudata* was found. This last species is rare in the island (Hynes 1952). It would seem, therefore, that there is no correlation between the macroscopic flora and fauna of the streams and the presence or absence of *Gammarus duebeni*.

LABORATORY INVESTIGATIONS

Considerable numbers of shrimps were kept in captivity in Liverpool in order to investigate details of the life history and the influence of the chemical composition of the water. The method used was a modification of that described by Sexton (1928). The animals were kept in water about 1 cm. deep in shallow enamelled dishes 25×30 cm. and 5 cm. deep, covered with a sheet of glass. They were fed on dead, naturally shed, leaves of elm as recommended by Sexton. Other foods were tried, including living *Nasturtium officinale* and *Riccia fluitans* and chopped earthworm, but as these were less convenient, and appeared to have no influence on the results obtained, elm leaves were adopted as the standard foodstuff. On this diet *Gammarus duebeni*, *G. pulex* and *G. z. zaddachi* were successfully reared through two generations, and the leaves were also found to have very little effect on the pH of even very soft waters. The dishes were kept at room temperature and examined at frequent intervals,

and the water was changed, or made up to a depth of about 1 cm. with distilled water, as necessary. Observations were conducted over a period of three years, during which over 200 batches of *Gammarus* were kept under observation, often for periods of longer than a year. The work was in two parts.

(1) Study of breeding, in which adults from the field, or more rarely from stock cultures, were placed in various waters and were watched to see if they bred.

(2) Study of survival and growth to maturity of young in different waters.

It was early found that both adults and young would live for many weeks in almost any fresh or brackish water, that the adults would mate and often lay eggs, eggs already laid would hatch, and the young would grow. This could not, however, be taken to indicate that the water was suitable for them, as in many waters the eggs laid there failed to hatch, and the young born there became weak and died after growing to a length of about 4 mm. Therefore breeding was only regarded as successful if young were produced from eggs actually laid in the water being investigated, and rearing, if the young specimens became fully and actively sexually mature. As this often took several months there were many occasions when an experiment failed, although in other similar dishes breeding or rearing were successful. Trials were therefore always at least duplicated, and failures were repeated many times before the results were accepted.

In the breeding tests five or six pairs of adults, none of which were ovigerous, were used in each dish, and often, once the females were seen to be carrying eggs, most of the males were removed to prevent their further interference. In the rearing tests 40–50 newly emerged young, hatched if possible in the water in which they were to live, were placed in each dish.

The results can be summarized as follows: *G. pulex* bred and matured successfully in Liverpool tap water (a soft water with about 13 mg. Ca/l.), hardened tap water (to which $CaCO_3$ had been added) and Port Erin stream water. It failed consistently to survive for long in 10 and 20 % sea water (diluted with glass distilled water). *G. duebeni*, of both fresh and brackish water origin, bred and matured successfully in 20 % sea water and 20 % artificial sea water (made from a recipe given by Sverdrup, Johnson & Fleming 1942) and bred successfully in 2 and 4 % sea water. It also bred and matured in 20 % sea water which before dilution had been boiled until it was reduced to half its volume. All of many attempts at breeding and rearing in Liverpool tap water, hardened tap water, Port Erin stream water and Rushen stream water failed, although one specimen, out of several hundreds tried, did just survive to maturity in Port Erin stream water. When, however, pure sodium chloride was added to Port Erin stream water, in amount sufficient to make the chloride content equal to that of 20 % sea water, both breeding and rearing were successful. A few artificial 'fresh waters' were also tried without success. *G. z. zaddachi* was successfully reared through two generations in 20 % sea water.

The failure of *G. duebeni* to breed in the water of the stream from which it was collected was surprising, especially as it had bred so readily in 20 % sea water, which was almost always successful and so came to be regarded as the control. Accordingly, Dr Jones undertook to try to breed the species, under similar conditions, in the stream water at the Port Erin laboratory. He tried specimens from the stream and from Gansey beach, and used 20 % sea water as the control. The shrimps from both habitats

bred in the brackish water and those from the stream bred in the stream water. Those from the beach did not, although eggs were laid. The successful breeding in Port Erin and its consistent failure in Liverpool remains unexplained. There were two differences in experimental conditions, either of which might have accounted for it. The temperature in the room at Port Erin where the tests were made was low (*c.* 7° C.), and the dishes were not covered with glass. It is possible therefore that they received some salt from the air, as the building is often showered with sea spray.

Further experiments were made in Liverpool in a cold room (at 7° C.) and in an unheated outhouse. In the cold room, which was dark, no breeding occurred even in 20 % sea water, and in the outhouse the results were almost the same as in the heated laboratory. The only difference was that in one of the artificial 'fresh waters' (0·33 % sea water + 150 mg. $CaCO_3$/l.) the shrimps bred and matured, whereas they had failed to do so in the laboratory. This water in its content of chloride, sulphate, calcium and magnesium ions roughly resembled that of Port Erin stream water (Tables 6 and 7), but they did not breed in the latter.

Apart therefore from the trial made in Port Erin, these results seem to show that *G. duebeni* will breed and mature readily in still water of high ion content, but not in normal fresh waters. That no trace elements or organic compounds are involved in their ability to breed in still brackish waters is shown by the fact that artificial sea water, made with pure salts, and boiled sea water, in which many complex organic substances must have been destroyed, were as effective as sea water itself, and that the mere addition of sodium chloride to Port Erin stream water changed it into a suitable breeding medium.

The trial made in the outhouse indicates that temperature was not a factor of importance in these experiments. It would seem therefore that, as the species breeds in freshwater streams, fresh water to be suitable must be moving. This is indeed also indicated by Kinne's recently published work (in press), on the osmoregulation of the species. Unfortunately it has not so far been possible to conduct suitable experiments with running water in Liverpool, but it is hoped to do so shortly.* It is perhaps significant that the species, unlike *G. pulex* which is sometimes found in ponds, has not been recorded from any still freshwater habitat, apart from large lakes where wave action would be a substitute for current, and that in the one place where it was found in small pools in the bed of a stream no breeding whatever was occurring (Fig. 8 *h*).

That the species will breed in running fresh water in the laboratory has been shown by Dr Frost, who has very kindly allowed me to quote her results. Specimens collected from fresh water in Co. Kerry were taken, in February 1939, to the Wray Castle laboratory of the Freshwater Biological Association, and were kept in various containers in still water. No breeding occurred, and finally they were placed in running water on the apparatus described by Worthington (1939), and young were produced between 17 May and early July. They did not survive to maturity, although four lived and grew until 3 October. No check was made to see if the females were ovigerous, but the shrimps were kept at a mean temperature of about 14° C., and at this temperature incubation takes about 20 days; the young were certainly therefore produced from eggs laid in captivity. When a similar experiment was tried with Liverpool

* See note on p. 84.

tap water the shrimps died within 48 hr., and showed the swoollen blue gills typical of exosmosis. In still tap water they lived for weeks, so it would seem that Liverpool water has too low an ion-content to be suitable even when flowing, and that the shrimps can only survive in small volumes of it when it is still, by loss of salts from their food and bodies.

Throughout the experiments conducted in the Liverpool laboratory, maximum and minimum temperatures were recorded. These varied from 5·5 to 32·2° C., but most of the time were between 10 and 25° C. The mean weekly temperature was about 12–13° C. in winter and 22–24° C. in late summer, and so was considerably higher than in the field (Fig. 9). Despite this, however, it was noticed that, irrespective of the time when experiments were started, young were never born during July, August and September, although they were produced in all other months. This corresponds almost exactly to the close season observed in brackish water in the field, but unfortunately I was not at the time aware of Kinne's work, and did not examine the oostegites of the females to see if they had lost their bristles. This was, however, the hottest period of the year in the laboratory (mean temp. above 20·5° C. and weekly maximum above 26° C.), and did not follow a fall in temperature such as Kinne found to precede his resting period.

DISCUSSION

Although the results of this study are in some respects incomplete and unsatsifactory it is possible to draw certain general conclusions from it. The suggestion that distinct physiological races of *G. duebeni* occur in freshwater and brackish water seems not to be tenable, both from field data and laboratory investigations.

G. duebeni is found in brackish waters round all Atlantic coasts northwards from the north coast of France. Its southern limits would appear therefore to be due to temperature, and there is, in fact, some indication that in brackish water breeding is inhibited by the effects of high summer temperatures. Presumably therefore, in the warmer parts of its range, the breeding period is short, and becomes too short farther south. A mean annual temperature of about 10° C. (Brittany) seems to be about its southern limit. It appears only to invade fresh waters in areas where *G. pulex* is absent, but is not found in fresh water in regions where winters are severe, even though *G. pulex* is absent, e.g. Norway (Stephenson 1940*c*) and Greenland. It occurs, however, in fresh waters of all such places as have an 'Atlantic winter', e.g. Cape Breton island, Iceland, Faroes, Shetland, Ireland, etc. In fact its northern freshwater limit seems to be about 5° C. mean annual temperature. Its northern brackish water temperature limit is not determinable, but as it is recorded from northern Siberia, where the mean July temperature is only about 10° C., it can obviously withstand considerable cold, although Forsman (1951) has shown that the shrimps cannot survive being frozen solid. That *G. duebeni* does not normally occur in fresh water on the same land mass as *G. pulex* indicates that competition occurs between the two species. It has already been suggested by Segerstråle (1950) that *G. duebeni* is excluded from the sea by marine competitors, and Jones (1948) and Forsman (1951) have suggested that its absence from some fresh waters may be due to competition with *G. pulex*. The present study shows that the food of both species is similar, and that they definitely tend to

occur in the same type of microhabitat, but nothing can be suggested as to how such competition operates. It has not been possible to study this in the laboratory as, under the conditions available, the two species could not be induced to breed in the same water, but they were observed to live together without mutual interference for periods of several weeks.

The Isle of Man and the Lizard peninsula appear to be the only exceptions to the general rule. In the former *G. pulex* is probably a recent introduction, but the Lizard, although almost an island, is in a different category. It would seem, however, that this anomaly can be explained in geological terms. If one assumes that *G. pulex* is of continental European or Asian origin, which seems reasonable in view of its wide distribution, north as far as southern Sweden (Oldevig 1948) and east as far as India, and of its varied races in these continents (Schellenberg 1942), and that it was absent from Britain during the Pleistocene ice-ages, it could have entered Britain, without crossing the sea, only during the period of the land-bridge across the Channel. Trusheim (1943) discusses the history of this bridge in considerable detail, and gives a map showing the coast-line and water-courses, during the period of lowest sea-level, 7000 to 8000 years ago. He states that about 6000 years ago the bridge disappeared and the Channel was formed. It would seem certain that, at the time of the bridge, the Thames was a tributary of the greater Rhine, which emptied into a brackish strait south of Doggerland, and that the major rivers north of this (Wash and Humber) also flowed into this strait, but were not in direct freshwater contact with the Rhine. It seems also that the Sussex rivers, but probably not the Test and Itchen, were in direct freshwater contact with the Channel river, and so with northern France.

If *G. pulex* was present in north-western Europe 8000 years ago, and was unable to cross the sea or brackish water, it could only have entered the Thames basin and a few smaller rivers, such as the Yare, to the north, and the Sussex rivers as far west as the Arun. From the laboratory experiments it seems that this species can tolerate very little sea water (cf. also Beadle 1943), and, although Widmann (1935) has shown that it is possible slowly to acclimatize specimens to 1% sea water, this salinity is not high enough to allow of passage from one river to another. The crossing of watersheds is also difficult for a creature with no resistant resting stage, and for *G. pulex* this would appear to be particularly difficult. Unlike *G. duebeni* (Segerstråle 1946) it does not voluntarily leave the water, it cannot withstand desiccation, it is too active, especially when adult, to adhere to the legs of a bird, and it is bisexual and the males do not search actively for the females. The crossing of a watershed and establishment on the other side must therefore be a rare event, depending on such things as severe floods.

The present westerly limit of *G. pulex* in Britain is the Lizard, and its northerly limit is apparently in West Ross-shire (Reid 1951). It is instructive to compare the numbers of watersheds which the species may be supposed to have crossed to reach these limits. From the Arun to the Lizard the number is about 12, via the Test-Itchen, Avon-Stour, Parret, Exe, Teign, Torridge, Fowey, Fal and three small streams between the Fowey and the Lizard. From the Thames or Yare northwards to West Ross-shire the number of watersheds is, very surprisingly, almost the same, if one counts, as seems reasonable, the Wash rivers as one. These rivers were until historical times linked by marshland and swamp. Here the rivers involved are the Wash, Humber (although this

may have received *G. pulex* before being severed from the Wash), Tees, Eden, Tyne, Tweed, Clyde, Loch Lomond basin (which is not and presumably has not for a long time been in freshwater contact with the Clyde), Forth, Earn-Tay and Caledonian canal area, whence one further watershed leads to the rivers of West Ross-shire.

So it seems that, in any given direction, *G. pulex* has been able to cross only about twelve watersheds in about 6000 years. It is of course possible that it reached these extreme points long ago, but there is no reason for believing that this is so, nor that it could not inhabit streams farther south or west of its present limit in the Lizard, or farther north than Ross-shire. In this connexion it may be relevant to note that until recently *G. pulex* was absent from Jutland north of the Limfjord (Stephensen 1940*c*; Kaiser 1941) but that it has been successfully introduced there. At no post-glacial time was north Jutland in direct freshwater contact with any major European river, and the Limfjord must have been formed at about the same time as the Channel.

The broad picture of the British distribution of *G. duebeni* and *G. pulex* can therefore be reasonably explained on geographical grounds, but the absence of *G. duebeni* from streams where it might be expected to occur cannot at present be accounted for. There are areas, such as Land's End, the northern half of the Isle of Man and the north of Scotland, where *G. pulex* does not occur, probably because it has not yet got there, and where one might therefore expect to find *G. duebeni*, but does not. Laboratory work indicates that in fresh but not in brackish water some movement is necessary for reproduction in *G. duebeni*. Fairly intensive study of water chemistry, temperature and associated fauna of streams in the Isle of Man, and of water chemistry of streams on the Lizard peninsula, has shown nothing which will account for the absence of this species from many apparently suitable localities. Similar study in Anglesey has shown that water chemistry does not explain the detailed distribution of *G. pulex*. At first sight it would appear that *G. duebeni* in streams on the Lizard peninsula and the Isle of Man was dependent on sea spray carried inland by the prevailing southerly winds, but that this is not so is clear from its wide distribution in Ireland and its absence from the equally spray-swept Land's End peninsula. It may be noted here that Steusloff (1943) also was unable to account for the absence of *G. pulex pulex* and *G. p. fossarum* from apparently suitable waters in Germany.

The breeding cycle of *G. duebeni* have been shown to be different in fresh and brackish water, there being a marked close season in the latter in late summer and autumn, which was not found in the former. It seems that this is largely because of higher summer temperatures in brackish water, although it is clear from the recent work of Kinne that the effect of temperature on the breeding cycle is not a simple phenomenon. The fact that no non-breeding mature females were found in the British populations during the close season, whereas such females are common in Germany, seems to be due to lower temperatures in early summer in the British localities.

The question if and how *G. pulex* can supplant *G. duebeni* in freshwater habitats is one which can best be solved by field experiments, and these have been tried in the Isle of Man, but so far with limited success. In July 1949 about 250 adult specimens of *G. pulex* were introduced into each of two small streams (Fig. 2, nos. 8 and 10), in which *G. duebeni* was present. These streams were carefully searched at intervals during the next three and a half years but no trace of *G. pulex* was found. In April

1952 a further 2000–3000 *G. pulex* were put into Spaldrick stream (Fig. 2, no. 8), but in July and the following April none could be found, although *G. duebeni* was still abundant. It is possible, however, that this was as yet too early to be certain that the second lot of *G. pulex* had not established itself. In July 1952 a further stream (Rhenwyllan stream, Fig. 2, no. 14), in which *G. duebeni* was abundant, was innoculated with 2000–3000 *G. pulex*, and this stream and Spaldrick stream are still under observation, although up till April 1953 no specimens of *G. pulex* have been recovered. In September 1949 about 250 *G. pulex* were placed in Rushen stream (Fig. 2, no. 15), and a further 50 were introduced in March 1950. No *Gammarus* had ever been found in this stream, and none were found there in January and April 1951. In March 1952, and again in July, *G. pulex* was found to occur sparsely from about 100 m. to about 300 m. below the point of introduction, and in April 1953 the population extended many hundreds of metres both above and below this point. Active breeding was in progress, and it seems certain that this population was the result of the introductions. This success in a stream to which *G. duebeni* has easy access from Gansey beach, but into which it had not penetrated, shows that *G. pulex* can inhabit a stream which for some reason is unsuitable for *G. duebeni*. A similar introduction of *G. pulex* was made in March 1950 into Fleshwick stream (Fig. 2, no. 7), which was also without *Gammarus*, but up to July 1952 no specimens had been recovered.

It seems therefore that introduction experiments cannot be expected to give rapid results, and work along these lines is continuing.

ACKNOWLEDGEMENTS

This study has involved much work confirming and obtaining new records of the distribution of *Gammarus* in British fresh waters, and I have been very greatly helped in this by many people.

Dr N. S. Jones has accompanied and transported me on many occasions in the Isle of Man, collected monthly samples, and made some laboratory observations for me; his help has been quite invaluable. Prof. J. B. Cragg, Mr G. I. Crawford, Mr G. Fryer, Dr J. A. Kitching, Mr R. MacDonald, Mr K. A. Pyefinch, Mr D. M. Reid and Dr G. M. Spooner have very kindly supplied me with many records from their own notes. Mr G. J. Arthur, Miss R. M. Badcock, Mr E. S. Brown, Dr R. W. Butcher, Dr W. E. Frost, Mr A. Gibson, Dr C. F. Humphries, Dr J. W. Jones, Miss E. Judges, Dr S. Lodge, Dr T. T. Macan, Mrs N. McMillan, Prof. H. P. Moon, Mr W. R. Munro, Prof. A. D. Peacock, Dr C. F. A. Pantin, Dr T. B. Reynoldson, Miss E. Sandison, Mr D. E. Sergeant, Dr A. J. Southward, and Mr A. Stout have either collected specimens for me or arranged for collections to be made. Dr W. E. Frost has also given me access to notes she made on *G. duebeni* in Ireland and on her attempts to breed it in the laboratory. To all these people I tender my very sincere thanks.

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SUMMARY

1. Literature on the ecology and distribution of *G. duebeni* Lillj. is briefly reviewed.

2. In Britain *G. duebeni* occurs in brackish water all round the coasts, but in fresh water only on the western and northern islands; it is not normally found in fresh water on the same land mass as *G. pulex*, which is almost confined to the British mainland.

3. The only two areas where both species occur in fresh water were studied in detail. On the Lizard peninsula the areas occupied are not contiguous. In the Isle of Man their areas overlap and in two streams they were found together. It is suggested that *G. pulex* is a recent introduction into the island.

4. Investigations on interbreeding, osmoregulation, kidney structure, size, and number and size of eggs have produced no support for the suggestion that there are distinct physiological races of *G. duebeni* in fresh and brackish water.

5. The diets of *G. pulex* and *G. duebeni* are shown to be similar.

6. The life cycles of *G. duebeni* in fresh and brackish water were found to differ; it is suggested that this is because of slight temperature differences.

7. Investigations of geology, dissolved salts, temperature, and associated flora and fauna have failed to explain why *G. duebeni* does not occur in all streams in areas where it is found. These investigations throw some doubt on the accepted ideas about the importance of dissolved salts to *G. pulex*.

8. In the laboratory it was found impossible to induce *G. duebeni* to breed and mature in still fresh water, although it did so in waters of relatively high ion content. It seems that the species needs running fresh water in order to complete its life cycle.

9. It appears that *G. duebeni* is potentially able to colonize certain types of fresh water, but that it is unable to do so in face of competition from *G. pulex*. It is suggested that the latter is extending its range in Britain and that when it arrives on a new land mass it eliminates *G. duebeni* from fresh water. Introduction experiments to investigate this are in progress.

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* Papers quoted only at second hand.

NOTE ADDED IN PROOF (see p. 76)

Since this paper was written specimens from both fresh and brackish water have bred in Liverpool in running water from Port Erin Stream; the young did not survive to maturity although they lived for several months.

OBSERVATIONS ON A HIGH-LEVEL POPULATION OF LIMPETS

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(With Plate 1 and 6 Figures in the Text)

INTRODUCTION

A population of limpets which occupied an unusually high level of the shore was discovered on the end faces of the breakwater at the entrance to Aberystwyth harbour. The numbers and distribution of these limpets appeared to be determined largely by the amount of sunlight experienced on the different faces, and since this varies between winter and summer it was suspected that changes would occur in the distribution of the population. Observations were therefore made on the variation in the numbers of limpets and their vertical distribution throughout a 12-month period. Some incidental information about the movement of limpets was also obtained and is included in this paper.

At the end of the breakwater there are a series of concrete faces (Fig. 1). The end face points approximately north-west and is 26 ft. long at the base. There are two corner faces, one pointing to the south-west and the other to the north. Between

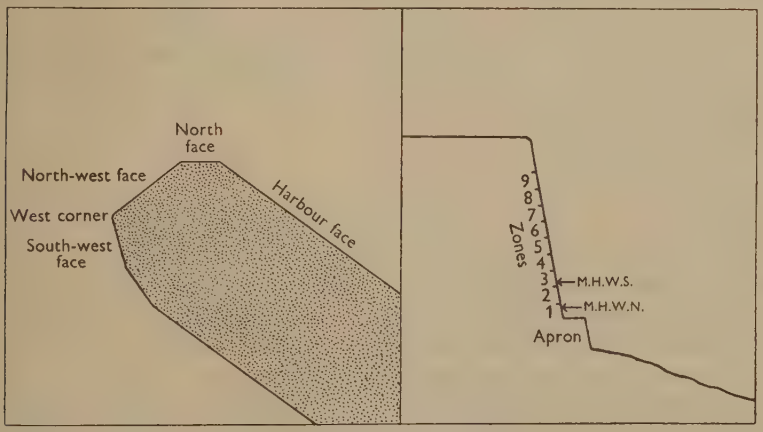

Fig. 1. (*a*) Plan of the end of the breakwater; (*b*) profile of the north-west face.

the north-west and the south-west faces there is a narrow corner face only 7 in. wide, facing west. All the faces incline inwards slightly towards the top of the breakwater. Below the south-west, west and north-west faces is an apron almost 3 ft wide, and below this a drop to a platform of concrete, and then rock, boulders and a limited amount of shingle. The faces rise 22 ft. above the apron and the levels of mean high

water of neap tides and mean high water of spring tides are 1·4 and 4·5 ft., respectively, above the apron which formed the base-line for all measurements.

The end of the breakwater is subject to almost continuous pounding by waves, the majority of which strike first against the west corner and south-west face, and the rocks and apron immediately below. On the north-west face there is a slight decrease in the amount of splash and wave action moving towards the north end. On relatively calm days waves splash up most of the end face from half to full tide, and in stormy weather the waves break right over the end of the breakwater making it completely inaccessible. This water collects in shallow pools on the flat top of the breakwater, and unevenness in the surface leads some of it to drain away down the end face about one-third of the distance along from the west corner.

The area immediately below the end of the breakwater can only be approached by walking along the rocks at low water of spring tides. On calm days 3–4 hr. may be available for inspection of the end face, but often heavy seas limit the time to as little as 1 hr. On such occasions it was impossible to complete the plotting of the distribution of the limpets in 1 day. The figures and results presented here are, however, limited to those days on which a complete count could be made.

For survey purposes the north-west face was divided into nine horizontal zones, each 2 ft. deep (see Fig. 1). Zones 1–4 were marked by paint, while the upper ones were delimited visually by reference to constructional marks in the concrete surface. During April six compact groups of limpets, comprising 252 individuals, were marked with a characteristic symbol (blue or white stripes, etc.), the paint being strictly confined to the shells of the animals. These groups were distributed in zones 1–5, the limpets above these levels being beyond reach. Further limpets were marked for specific purposes which will be described later. Apart from this initial marking with paint, and the touching of the shell with chalk when being counted, the limpets were disturbed in no other way. After observations were discontinued a sample of 100 limpets was removed for identification. Ninety-eight were *Patella vulgata* L. and two were *P. depressa* Pennant.

OBSERVATIONS

(*a*) *The distribution of limpets in April 1951*

Observations were confined to the south-west, west and north-west faces, except when following the movement of marked individuals on to other surfaces. On 5 April the distribution of various plants and animals was as follows. Except for two grazed areas the south-west face was covered by algae. A thin continuous film of Myxophyceae covered all levels while an additional growth of *Porphyra*, *Enteromorpha* and *Bangia* was present in the lower part. The latter died away in the summer, but the Myxophyceae persisted throughout the year. Adjacent to the west corner all the algae had been severely grazed to a distance of 1–2 ft. from the corner, and to a height level with zone 9 on the north-west face. Scattered at various heights within this grazed strip were 31 limpets, the only ones present on this face. A very narrow strip along the bottom of the face had apparently been grazed by limpets present on the adjacent apron, but none of these were ever found on the face itself. On the narrow west

corner there were 62 limpets, mainly in zones 4, 5 and 8. The film of Myxophyceae was present in and above zone 9, and there were a few barnacles in zone 1.

On the north-west face there were 2452 limpets and their vertical distribution can be seen from Table 1. In general the highest levels were reached in the western half of the face, a feature which was maintained throughout most of the year and which

Table 1. *The distribution of limpets on the breakwater throughout the period of observations*

	Zones of the north-west face								Totals			
	1	2	3	4	5	6	7	8 and above	North-west face	West corner	South west face	Grand total
5 Apr.	137	613	743	688	167	38	45	21	2452	62	31	2545
21 May	85	867	801	454	127	34	19	0	2387	55	24	2479
3 June	123	892	761	463	111	28	9	0	2387	78	22	2487
6 June	117	938	700	410	90	26	8	0	2289	77	12	2378
21 June	147	1053	671	33	0	0	0	0	1904	45	9	1958
4 July	178	923	521	17	0	0	0	0	1639	66	4	1709
20 July	217	933	581	29	1	0	0	0	1761	60	0	1821
4 Aug.	252	848	568	74	1	0	0	0	1743	57	30	1830
18 Aug.	346	784	522	121	1	0	0	0	1774	35	50	1859
Sept.	—	—	—	—	—	—	—	—	—	—	—	—
5 Oct.	125	570	327	378	203	30	8	0	1641	97	164	1932
17 Oct.	204	593	273	435	140	33	10	1	1689	92	196	1977
13 Nov.	174	527	304	403	185	79	41	3	1716	128	172	2016
29 Nov.	155	539	324	434	188	88	59	2	1789	161	43	1993
13 Dec.	154	499	323	370	194	132	83	5	1760	160	18	1938
12 Jan.	126	482	298	318	182	99	150	72	1727	146	5	1878
26 Jan.	97	489	234	302	171	124	180	24	1621	135	4	1760
11 Feb.	119	476	299	311	160	131	188	37	1703	110	3	1816
25 Feb.	137	488	306	287	157	114	118	98	1705	116	13	1836
25 Mar.	164	522	367	347	151	53	71	50	1725	116	18	1859
15 Apr.	172	628	376	281	98	49	64	20	1688	75	32	1795
14 May	218	617	434	295	69	24	42	5	1704	113	50	1867

appeared to be related to the moister conditions prevailing in that half. A film of Myxophyceae covered the upper levels and extended as low as zone 5 in parts of the northern half of the face. The division between the limpet and myxophycean areas was marked by a sweeping irregular line, the position of which showed clearly the grazing activities of the nearest groups of limpets. In zones 1 and 2 there was a prolific growth of *Bangia, Porphyra* and *Enteromorpha*, with smaller amounts occurring in zones 3 and 4, and the various groups of limpets stood out conspicuously in the middle of grazed clearings. The general pattern of the distribution of the algae and limpets in April is shown in Fig. 2.

Although no detailed check was made on the size of limpets in relation to their vertical distribution, a visual estimate of size showed that the smaller individuals (less than 20 mm. approximately) predominated in zones 1–3, that the numbers of large and small were almost equal in zone 4, and that the small limpets then became increasingly scarce and were completely absent from zones 7–9. This pattern of distribution in relation to size confirms the observations of other authors (Das & Seshappa 1948, Jones 1948).

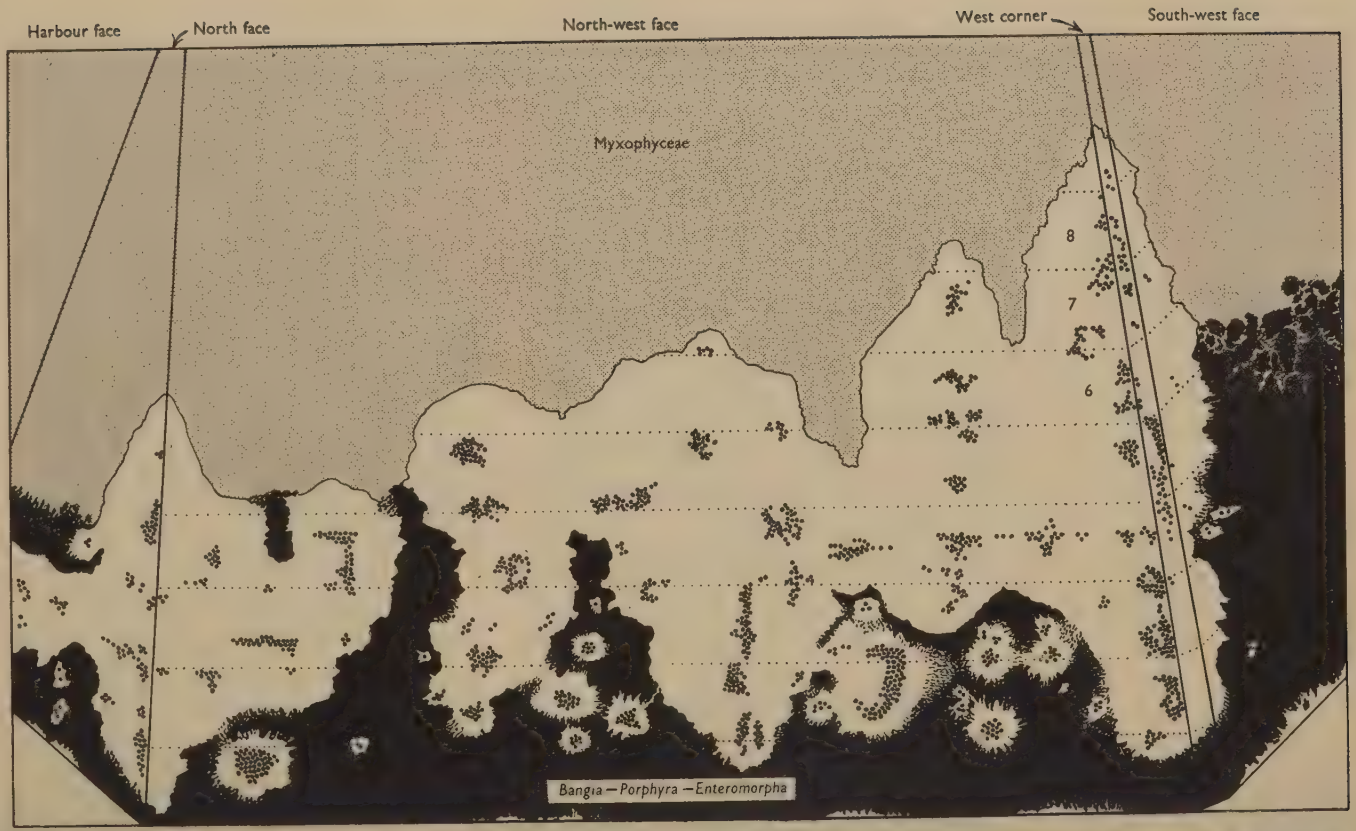

Fig. 2. A diagrammatic representation (based on photographs) of the end faces of the breakwater showing the distribution of Myxophyceae, limpets and algae on 5 April. The relative size of the more important groups of limpets only is shown, not the actual numbers involved.

The relatively low numbers of limpets in zone 1 at all times was probably related to several features: the longer persistence of the algae in this zone, the presence of moderate numbers of barnacles and the rough pitted nature of the surface in some places. Moreover, those limpets lying inside the main barnacle population, at the junction of the face with the apron, were not included in the counts.

Balanus balanoides occurred intermittently in zone 1 and the lower part of zone 2, and newly settled spat were distributed throughout zones 1 and 2, and in small quantity in zone 3. There was no clearly defined 'barnacle line' and *Chthamalus* was very scarce. No Fucaceae grew on the three faces under observation.

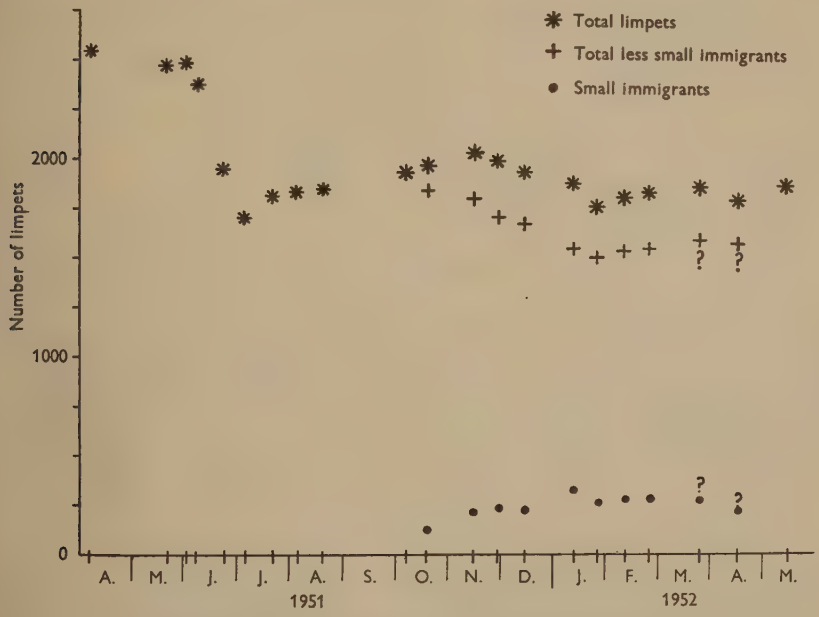

Fig. 3. Changes in the total numbers of limpets during the 12-month period.

(*b*) *Change in numbers*

As the area under observation was not completely isolated, changes in the numbers present could have been caused by migration both into and out of the area. The marked individuals showed that migration off the faces was occurring, for of the 199 which could still be identified by January 1952, 39 were found on the rocks below the breakwater or on faces inside the harbour. Frequent small fluctuations in the total number of limpets present may therefore have had little significance, but some of the changes in numbers merit attention for they appear to have been caused by particular events or were part of a seasonal trend.

The total numbers involved can be seen from Table 1 and are plotted in Fig. 3. From the original number of 2545 on 5 April there was a slight drop till the beginning of June, when several sharp falls reduced the total to only 1709 on 4 July. Thereafter,

numbers recovered gradually by over 300 until November, when a slight downward and irregular trend began and continued until the end of observations.

The mortality in June appeared to be caused by a chance combination of conditions which were all unfavourable for the high-level individuals. During late May and June two periods of neap tides coincided with calm, sunny weather and offshore winds. Splashing of the upper levels was thus greatly reduced and moreover, direct sunlight was now falling on the north-west face from mid-afternoon onwards. On 6 June, after the first period of neap tides, numbers had fallen very little, but even then at the

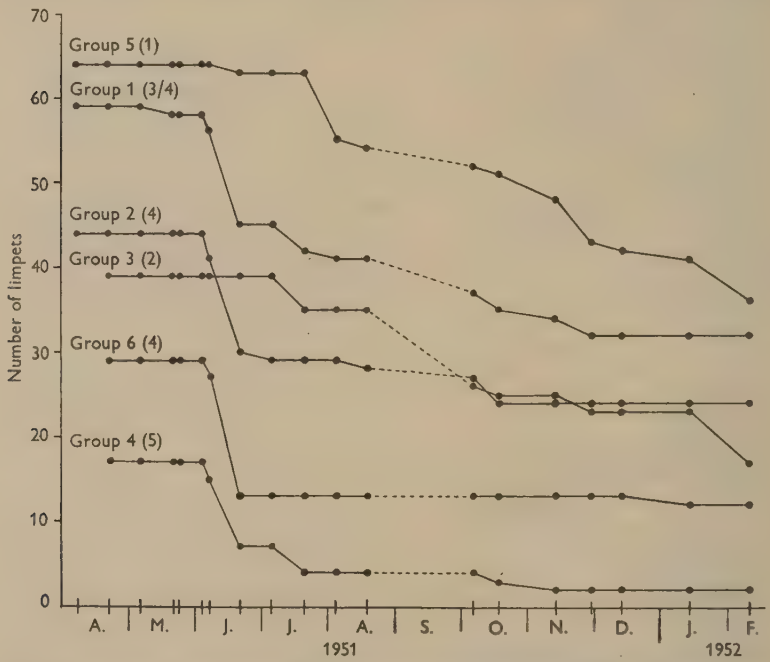

Fig. 4. Changes in the numbers of limpets in the marked groups. The figure in brackets indicates the zone which that group originally occupied.

lower, moister levels within reach, a slight brushing with the sleeve was sufficient to dislodge some limpets, and many shells were adhering only by dried mucus. In those shells which were accidentally dislodged the animals were dried and shrivelled. On 6 June the smaller individuals of zones 4–6 appeared to be the most affected, but by 21 June many of the larger animals, too, had succumbed or migrated. By this date, which was just after the second period of neap tides, the total loss in individuals since the beginning of the month was over 500. No animals had survived above zone 4, and even here there were only 33 in contrast to the 400–600 present on all previous occasions. This mortality continued throughout the month, and by 4 July the lowest total of 1709 was recorded.

While the disappearance of the population of zones 4–9 appeared to be due primarily to the death of these high-level individuals, it was also partly due to a number of them

migrating downwards. The total reduction in numbers on the north-west face between 6 June and 21 June was 385, but the loss of limpets from zone 4 and above was 501, a difference of 116. By 21 June the population of the lower zones had increased by 116, and while this exact balance of numbers may have been coincidental, it is nevertheless probable that approximately this number did survive as a result of moving to lower levels.

By 4 July there was a further loss of 265 individuals, mainly from zones 2 and 3. Of the six marked groups, those which had originally occupied zones 4 and 5 suffered little or no further loss between 21 June and 4 July (Fig. 4). This fact suggests that the bulk of the loss during this period was sustained by the population originally present in zones 2 and 3, rather than by the survivors which had moved down from higher levels.

Table 2. *The survival of the marked groups*

Group no.	Zone when marked	Original no.	No. on 21 June	No. on 11 Feb.
1	3–4	59	45	34
2	4	44	30	27
3	2	39	39	14
4	5	17	7	2
5	1	64	63	36
6	4	29	13	12

The mortality at different levels is illustrated by the fate of the various marked groups. From Table 2 and Fig. 4 it can be seen that the two low-level groups (nos. 3 and 5) suffered no loss during the June period, whereas the other groups at higher levels suffered markedly. In the case of group 4 in zone 5, over half the original number was lost, and the survivors had all moved to lower levels.

The higher groups, which consisted mainly of large animals, lost relatively few of their members after the June period, whereas the low-level groups (3 and 5), which consisted of individuals of all sizes and which were not affected in June, lost members steadily during the remaining period. In the last month these groups continued to lose individuals while the other groups remained constant and had been so for some time.

The numbers of surviving individuals shown in Table 2 refer to the total number which could be found on the north-west face and in its vicinity. In most cases between one-third and one-quarter of the survivors were found on adjacent faces, or less commonly on the rocks below.

Without previously marking all the limpets in the vicinity it was not possible to determine how numbers fluctuated as a result of migrations on to the faces from other areas. One type of migration could be checked however, for it was an upward movement of individuals which were less than 10–12 mm. in size and in many cases were as small as 5 mm. These limpets were first noticed on the north-west face in October and may possibly have appeared first at these levels in September, when I was away from Aberystwyth. Their numbers and vertical distribution were checked on all subsequent visits, and are shown in Table 3. Counting was suspended in April, when it had become increasingly difficult to distinguish between the larger of the newcomers

and the smaller members of the established population. A comparison of the total numbers with the number of new arrivals shows that even when the latter was increasing the total population was relatively stable or even decreasing (see Fig. 3). In this year (1951–52) the arrival of new limpets barely maintained the existing population, and did not make up for the high mortality of the early summer.

Table 3. *The distribution of small immigrant limpets*

	Zone						
	1	2	3	4	5	6	Total
5 Oct.	Present but not counted						—
17 Oct.	36	78	17	0	0	0	131
13 Nov.	51	118	20	16	0	0	205
29 Nov.	31	149	30	21	0	0	231
13 Dec.	25	113	37	39	0	0	214
12 Jan.	65	160	46	51	2	0	324
26 Jan.	47	127	39	39	4	0	256
11 Feb.	49	144	38	38	3	0	272
25 Feb.	64	137	37	41	2	0	281
25 Mar.	74	135	39	14	0	0	262?
15 Apr.	44	116	45	13	0	0	218?

The steady decline in the existing population after October is a well-marked feature for which there is no obvious explanation. Because of difficulties in distinguishing between the newcomers and the existing population, it is probable that in the early months of 1952 the numbers of the former were underestimated, in which case this decline was even greater. As will be seen later the main trend of movement was up the faces during this period, and so the decrease in numbers would appear to have been caused more by the death of the limpets than by their migration down to the rocks below.

(*c*) *Changes in vertical distribution*

Coinciding with the change in total numbers was a change in the vertical distribution of the limpets. To a large extent the disappearance of the high-level limpets in June was caused by their death, but migration also played a part, for the redistribution of the population involved greater numbers than those by which the population changed. From the first the fall in numbers in zone 4 and above was accompanied by a build-up in zone 2, where numbers increased from 613 in April to 1053 in June. After the summer there was a gradual extension of limpets into the upper zones, leading to a more uniform distribution over the face. Zone 4 which in late June and July was almost empty, contained 18–25% of the total population during most of the winter, and as many as 11% were present in zone 7 at one time (Fig. 5). After February a steady decline occurred in zones 5–9, comparable to that which was under way when observations first began; at the same time zones 2 and 3 showed an increase in numbers again.

This general pattern of movement, down the face in spring and summer and up the face in autumn and winter, is clearly shown by the marked groups which were originally in the higher zones. Most of group 1 lay in zone 4, and the vertical distribution of the survivors of this group at selected dates is shown in Table 4. After the

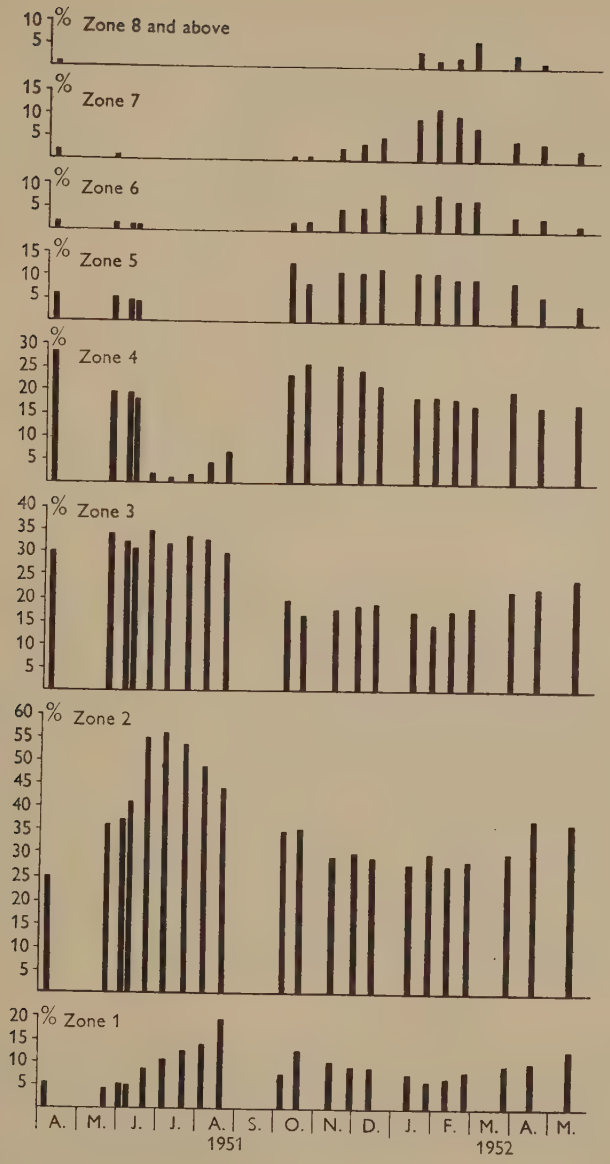

Fig. 5. Changes in vertical distribution as shown by the percentage of the total population present in each zone of the north-west face. The changes occurring between May and July reflect both the re-distribution and the death of the high-level limpets during that period, whereas the changes in the autumn and winter result mainly from the re-distribution of the existing population.

initial redistribution of individuals in June, the lower zones remained occupied until the general upward movement began in the autumn. By 11 February more than half of the survivors remaining on the face had moved up into zones higher than those originally occupied. The eight limpets no longer on the north-west face were mostly found on the north corner and harbour faces, and five of these were also on a level with or higher than their original position on the north-west face. Of the other high-level groups, 14 out of 20, and 6 out of 7 of the survivors still on the face, had moved to higher levels. In the cases of group 4 (zone 5) the two remaining survivors were last recorded in zones 7 and 8, after having spent the summer in zones 1 and 2.

Table 4. *The vertical distribution of limpets belonging to group 1*

		Zone							In other areas
	Total	7	6	5	4	3	2	1	
6 Apr. 1951	59	—	—	—	47	12	—	—	—
21 May 1951	59	—	—	—	37	16	5	—	1
6 June 1951	56	—	—	—	24	20	10	—	2
21 June 1951	45	—	—	—	3	21	19	—	2
18 Aug. 1951	41	—	—	—	5	17	19	—	—
5 Oct. 1951	37	—	2	11	8	4	5	—	7
13 Dec. 1951	34	4	1	5	5	6	2	2	9
11 Feb. 1952	34	6	4	4	4	3	3	2	8

This movement up to high levels was not confined to individuals which had originally occupied them. Members of the two low-level groups spread upwards in the autumn, but in both cases many survivors (22 out of 28; 7 out of 12) remained at the original level. To reveal upward movement by small individuals (less than 12 mm.) 100 limpets lying in zone 1 and the lower half of zone two were marked. During the summer there was little change, but in the autumn the movement became more pronounced, and by 17 October the 82 individuals which remained were distributed thus in zones 1–5: 9, 44, 11, 13 and 5. The upward dispersal continued throughout the winter and while approximately half of the survivors (63 in March) still occupied zones 1 and 2 in January, February and March, the other half was distributed in decreasing numbers up to zone 7. Although this upward movement of smaller individuals accompanied the return of the high-level limpets in the autumn, the smaller limpets did not usually reach the same height as the larger ones in the same month. Thus from January to March, when large animals were present in zone 9, the smaller marked ones reached only to zone 7.

A further form of migration up on to the north-west face was indicated by the intermittent appearance at various levels of large limpets with adult barnacles on their shells. None of the limpets originally in zones 1 or 2 had barnacles attached, so these particular individuals must have come from the apron or even from the rocks below.

The vertical movement on the west corner and on the south-west face was somewhat obscured by movement sideways from the north-west face. Moreover, because of the changes of aspect these two faces are less favourable habitats for high-level specimens. Trends similar to those on the north-west face could be seen here, but they occurred at a lower level, and so in the summer when zones 1–4 were occupied on the north-west face, limpets only reached to zone 2 at the corner and were absent

for a time from the south-west face. On the other hand, the autumn and winter conditions were very favourable on the well-splashed corner, and here the upward migration took some individuals almost to the top of the breakwater.

(*d*) *Movement of individuals*

The dispersion of a marked group either by vertical or sideways movement was not a slow, gradual process; a group might remain more or less intact (apart from slight positional changes within the group) for perhaps 4–8 weeks and then suddenly a few members would be found several feet away. Some would retain that new position for a time and then would move again, while others would move 1 or 2 ft. between several successive visits. Apart from the broad upward or downward movement of the population as a whole, the movement of individual limpets appeared to be haphazard, and some of the more active would move irregularly around and back across the original group site. 'Home-scars' of the type often found on rock were not present on the concrete faces. The nearest approach to a 'home' was a brownish stain which outlined the position of some of the larger limpets.

Two compact groups of ten limpets were numbered 1–10 in blue and white paint, and detailed records were made of changes in their position. The following examples indicate the variation which occurred in the movement of some of these individuals between April and 17 October, all 20 having changed position to some extent.

(i) No. 5, white: a change of 8 in. was observed on 5 May; on 26 May the specimen was 6 ft. away from the position occupied 48 hr. previously. Change of position occurred continuously in June, July and August, all the moves being haphazard and up to 4 ft. 6 in. in distance. By 5 October it had rounded the corner to the north face and was 15 ft. away, but on 17 October it was back on the north-west face within 6 ft. of its original position.

(ii) No. 6, white: after a variety of small moves which did not take it more than 6 ft. away from the original group area, this individual was found in August about 45 ft. away on the harbour face.

(iii) No. 9, white: this stayed in approximately the same area until 5 October, when it had moved 2 ft. higher.

(iv) No. 3, blue: a move of 3 ft. was recorded on 5 May, and by 21 June it had travelled another 9 in. only. Thereafter it occupied approximately the same position.

(v) No. 10, blue: this limpet moved 15 in. within 2 days of being painted; on 5 May it was 28 in. from the edge of the group and it had disappeared by 21 May.

DISCUSSION

(*a*) *Conditions influencing the limpet population*

Discussing the distribution of limpets, Orton (1929) concluded that 'strongly insolated habitats appear to be unviable as a result of the direct effect of the insolation on the animal', but suggested that a deficiency of food may also be a limiting factor of importance. Dealing with other shores in the Aberystwyth district, Evans (1947) found that the upper limit was determined by the orientation of a particular habitat and its exposure to splash and spray. In an extremely well-splashed, shaded situation he found limpets to a height of 15 ft. above M.H.W.S. Das & Seshappa (1948), on the other hand, placed the main emphasis for determining the upper limit of limpets upon the availability of algal food. The distribution of limpets on the end faces of the breakwater, and the variations observed during the year, leave little doubt that sunlight and

the amount of splash and spray experienced, determine the upper limits of this limpet population. The influence of these factors is increased by the occurrence of low water of spring tides in the afternoon here. The south-west face, although well splashed, is a very sunny position and so, apart from the few limpets which had wandered round the corner, remained largely unoccupied for most of the time. The bottom of this face, approximately 1·5 ft. below M.H.W.N., marked the upper limit of the population here. The west corner, receiving less sunlight than the south-west face, was a more suitable habitat, but even here there was a short period in the summer when limpets were restricted to zones 1 and 2. In winter this corner is very wet and the greatest height was reached here, a few limpets in zone 9 being almost 18 ft. above those lying along the base of the adjacent south-west face. These animals were about 13·5 ft. above M.H.W.S. The north-west face receives direct sunlight only in the late afternoon and evening in summer months, and being subject to considerable splashing also, it is the most favourable habitat on the breakwater. Even during the summer the population remained at a higher level than elsewhere. On the north and harbour faces some morning sunlight is experienced and wave action is very greatly reduced. Consequently the upper limit of the limpets falls considerably on rounding each corner from the north-west face, although it still remains higher than on the south-west face. Thus the vertical distribution around the end faces of the breakwater shows that where sunlight is excessive or wave action is reduced, the population is permanently restricted to a lower level; and where the amount of sunlight experienced varies from winter to summer marked seasonal variations occur in the vertical distribution of the animals.

The availability of food appears to be a lesser consideration. The south-west face was always covered by algae of one sort or another, but these were only grazed near to the west corner and the north-west face; the many limpets at this end of the north-west face were apparently feeding on the south-west face but leaving it before the tide receded completely. The number of limpets remaining on this face declined from thirty-one in April to none in July, but by October 191 were present and the grazed strip was now 4 ft. wide in places. Since the food supply here was always much greater than at the same height on the north-west face, it was expected that this new population would remain or even increase during the winter, but by the end of January only four individuals remained and numbers were small thereafter. While no reason can be advanced for this sudden decline in numbers, the event showed that availability of food did not alone determine the distribution of the population. Similarly, all the upper parts of the other faces and part of the flat top of the breakwater were covered by Myxophyceae in winter but these areas, too, were without limpets. On a variety of other shores in the British Isles ungrazed belts of Myxophyceae lie above the levels reached by limpets (personal observations), and it is concluded, therefore, that the presence of a suitable food supply does not in itself lead limpets to occupy a higher or more sunny level. However, the margins of such a food supply may, as on the breakwater, be grazed by limpets residing in a more favourable habitat.

The presence of algae did however have a temporary influence upon the local distribution of the limpets. While the densest growth of *Porphyra*, *Bangia* and *Enteromorpha* were present in March and April many groups of limpets stood out in

Part of the north-west face showing the grazing paths and cleared areas among the *Bangia* and *Porphyra*.

the centre of grazed clearings (Pl. 1). Although an occasional marked individual from a group surrounded by algae would be found several feet away, having wandered over the intervening growth, the numerous grazing paths in the algal mat showed that after grazing the majority of limpets were returning to the same group area. Even in zones 4–6 where the quantity of algae was less the groups tended to remain compact. There was no indication that the limpets ever massed along the edge of the ungrazed area and were slowly reducing it. When algae were less plentiful, however, and as the downward movement began the former distinctive grouping of many of the limpets

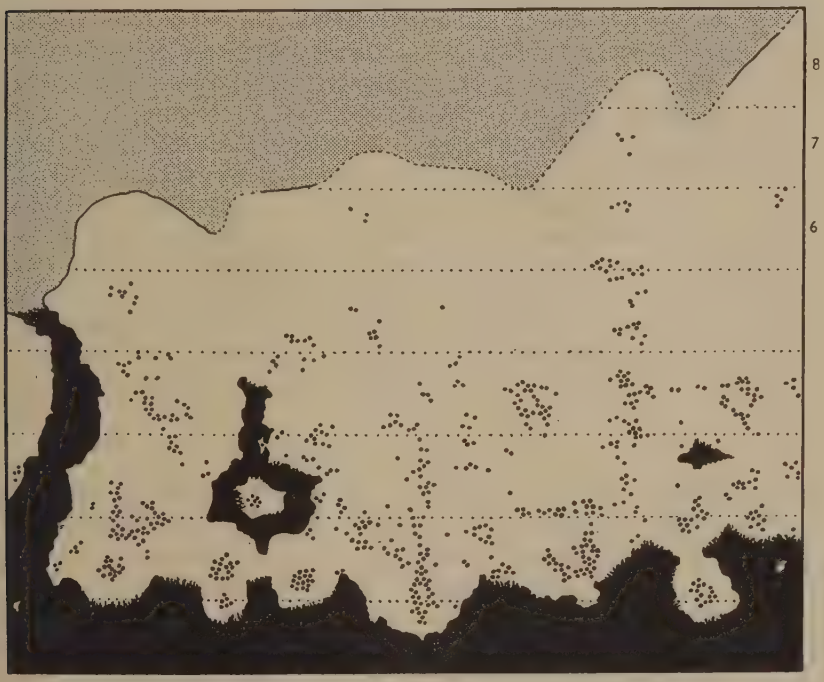

Fig. 6. A diagram (based on a photograph) of part of the north-west face on 6 June. A comparison with Fig. 2 shows how the groups of limpets have now become scattered. As in Fig. 2 no attempt has been made to show the actual numbers of limpets.

was lost (Fig. 6 and compare Fig. 2). In the following spring the growth of algae was on a very reduced scale compared with 1951, and, probably for this reason, the compact groups of several dozen specimens were less common than in the previous year.

While adverse physical conditions appeared to cause the high mortality in June, the steady fall in the numbers of the existing population after October remains unexplained. The deaths which are assumed to have caused this fall may have resulted from shingle being thrown against the faces during storms; or partly from the attacks of Oystercatchers which were once found to have removed a few marked limpets from the bottom of the north-west face. The mortality may have been a normal phenomenon at this

time of year. Orton (1928) states that the spawning period lasts from September or October to February or March, and it is possible that a regular fall in the population occurred as some individuals finished spawning.

(*b*) *The influence of limpets on the barnacle population*

On such an exposed habitat as the breakwater barnacles would be expected to occur in quantity to at least the level of M.H.W.S., if not several feet higher. In March and April 1951, however, intermittent patches of *Balanus* occurred only in zone 1 and the lower part of zone 2, 1–2 ft. below the level of M.H.W.S. The fate of the spat that season probably indicates why the barnacle population was so poor. The spat settled and metamorphosed in zones 1–3 wherever the growth of algae was not too dense. The reduced surface area which was available limited the possible population in the first instance, and then the spat which had settled on the weed-free areas suffered heavily from the movement of the limpets. First the young barnacles in the immediate vicinity of the limpet groups were dislodged, but gradually more and more disappeared. Eventually most of those which survived were ones which had settled on rough pitted surfaces or among established barnacles, and which were thus more protected in the early stages. The final increase in the total barnacle population was thus only very slight. Conditions the next year were more favourable in that limpets were fewer and the growth of algae was poor. Although this spatfall was not observed it was apparently more successful, for by November and December 1952, the patches of barnacles were larger and more numerous and extended in a few cases almost to the top of zone 2.

(*c*) *Vertical migration*

It has long been established (Russell 1907; Orton 1914) that the majority of large and medium-sized individuals return to a definite position after feeding excursions. Orton (1929) showed, however, that movement to a new position can occur on smooth damp surfaces, and more recently Jones (1948) has shown that the adults may move several yards to new sites, and even 30 yd. in one extreme case. It is not surprising, therefore, that movements to new positions were made on the breakwater, especially as 'home scars' were few in number. It is perhaps remarkable that the homing behaviour was so much in evidence under such damp conditions. Although movement was so frequent, some groups did occupy their original or new position for several months with only minor rearrangement of the individuals within the group.

The more interesting aspect of the movement is the vertical migration. Movement downwards in spring and upwards in autumn does not appear to have been recorded before, but knowing that changes of position occur frequently on the breakwater, the population would be expected to move, or else die, during adverse summer conditions; and both of these possibilities did in fact occur. Closer adherence in order to avoid desiccation must have proved fatal to many of the high-level limpets in June, whereas those which moved, or were able to move and did so in the right direction, probably survived this period. The return movement would follow from random wandering as the critical level rose again in the autumn. The upward migration of the small marked individuals may again be explained by random movement over the damp barnacle-free

surface, but there may also be a tendency to move upwards; for whereas on the last six occasions approximately half of the survivors (66 falling to 63) had moved up the face, only two were found below their original level.

The appearance of even smaller limpets in the lower part of the face in the autumn and winter again suggests an upshore trend in the movement of the young. Having no breeding data for this locality and year, it is difficult to estimate the age of these individuals. The size reached by limpets in their first year seems to vary greatly: Orton (1928) found lengths of 26–35 and 11–27 mm. at Plymouth in different years; Russell (1909) found lengths of 20–25 mm. in Scotland; and Jones (1948) gives 12·5 mm. as the average size at the Isle of Man after 12 months. Some of the smallest individuals which appeared on the breakwater may have settled in the positions in which they were first noticed very early in the breeding season, in September 1951. However, since the larvae are stated by Smith (1935) to settle when not more than 0·2 mm. long, the majority of these small limpets were presumably individuals from the previous breeding season, 1950–51; in this case they must have migrated up the shore from an area of dense barnacles.

The high-level population was thus maintained by three migrations up the face in autumn: the return movement of the surviving high-level limpets, the upward movement of the small marked individuals (and presumably others of all sizes), and finally the migration of very small limpets from levels below the breakwater. Much of this movement could have been random wandering after the onset of better conditions in the autumn, but a tendency to migrate upwards apparently existed in the movement of the younger individuals. In view of the many investigations, some of which have been summarized and discussed by Brian & Owen (1952), into anatomical and shell characters of limpets from different levels of the shore, it would be desirable to have further information on the movement of young limpets. The upward movement occurred here not at the upper splashed levels of the face but strictly within the normal tidal range, and may therefore be expected to occur at similar levels on other shores. Gowanloch & Hayes (1926) found that a negatively geotropic response in the behaviour of *Littorina littorea* was checked by increasing desiccation at the higher levels of the shore, and a similar type of mechanism may operate in the case of limpets. Little information was obtained about the movement of large individuals down to lower levels but this did occur and appeared to be on a smaller scale than the upward movement of the small animals.

The observations recorded here have shown that a population of limpets at a high level is very susceptible to changes in external conditions, and that both the numbers and distribution can vary appreciably from one season to another. The additional information which was obtained from these observations points to several aspects of the movement of limpets which require further investigation.

ACKNOWLEDGEMENT

It is a pleasure to record my thanks to Dr E. E. Watkin for his very helpful criticisms of this work.

SUMMARY

1. The level which limpets reach in the upper shore is shown to be dependent upon the exposure and the aspect of a locality. The presence of algal food does not in itself lead to the occupation of higher levels.

2. Seasonal variation in the amount of sunlight experinced on a particular situation leads to: (*a*) the death or downward movement of limpets from very high levels in spring and summer; (*b*) a return upward movement of limpets in autumn and winter.

3. There is some evidence of an upward trend in the movement of young individuals.

4. Considerable variation exists in the frequency with which individual limpets move to new positions on a barnacle-free surface.

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THE INFLUENCE OF THE GEBEL AULYIA DAM ON THE DEVELOPMENT OF NILE PLANKTON

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(With 3 Figures in the Text)

INTRODUCTION

Although the hydrology of the Nile has been thoroughly investigated by the Egyptian and the Sudan Irrigation Departments, the only detailed biological work published to date is on the algal flora of the lower reaches (Abdin 1946, 1947, 1948, 1949). During the past few years investigations on the middle and upper reaches have, however, been started by biologists from the University College, Khartoum.

The hydrological and, apparently, also the biological conditions of the river have been altered profoundly by man, and further considerable changes are yet to be made. The dams at Sennar (Blue Nile), Gebel Aulyia (White Nile) and Aswan (Lower Nile), in addition to the natural barriers, the cataracts and swamps, divide the river into regions, distinctive not only in their utilitarian and geographical aspects, but also showing specific biological features. The distances of 5611 km. from the Delta to Lake Victoria on the White Nile and the 4590 km. to Lake Tana at the head of the Blue Nile, render a biological survey of the river an immense task, and thus investigations must be carried out in sectors defined by natural conditions and transport limitations. One such sector is on the White Nile south of Khartoum (Fig. 1), where the Gebel Aulyia Dam converts the river into a shallow, slow-flowing 'lake', which in places is three miles broad. The dam, built in 1937 44 km. south of Khartoum, provides an irrigation reservoir for Egypt. Each July the dam is closed and the reservoir begins to store water; when full, normally by September, it holds $3{\cdot}5 \times 10^9$ cu.m. As a result, a rise in river level is recorded more than 500 km. upstream of the dam. Not until February is the dam fully opened to allow for the decreasing flow in the Blue Nile, and the water in the reservoir shrinks to normal river level by May. Strong southerly or northerly winds, according to the season, frequently produce impressive waves on this vast, open, temporary 'lake'.

The present paper examines the effects of the storage of this large volume of water on plankton production in part of the river upstream of the dam. A series of samples were taken from a place near Khartoum to beyond Gebelein, a distance of 396 km., samples and data being collected at eleven stations, separated by distances varying from 20 to 70 km. (Fig. 1). The river journey was completed between 13 and 18 December 1951, thus ensuring a reasonable comparability of samples in time, an important consideration in flowing water.

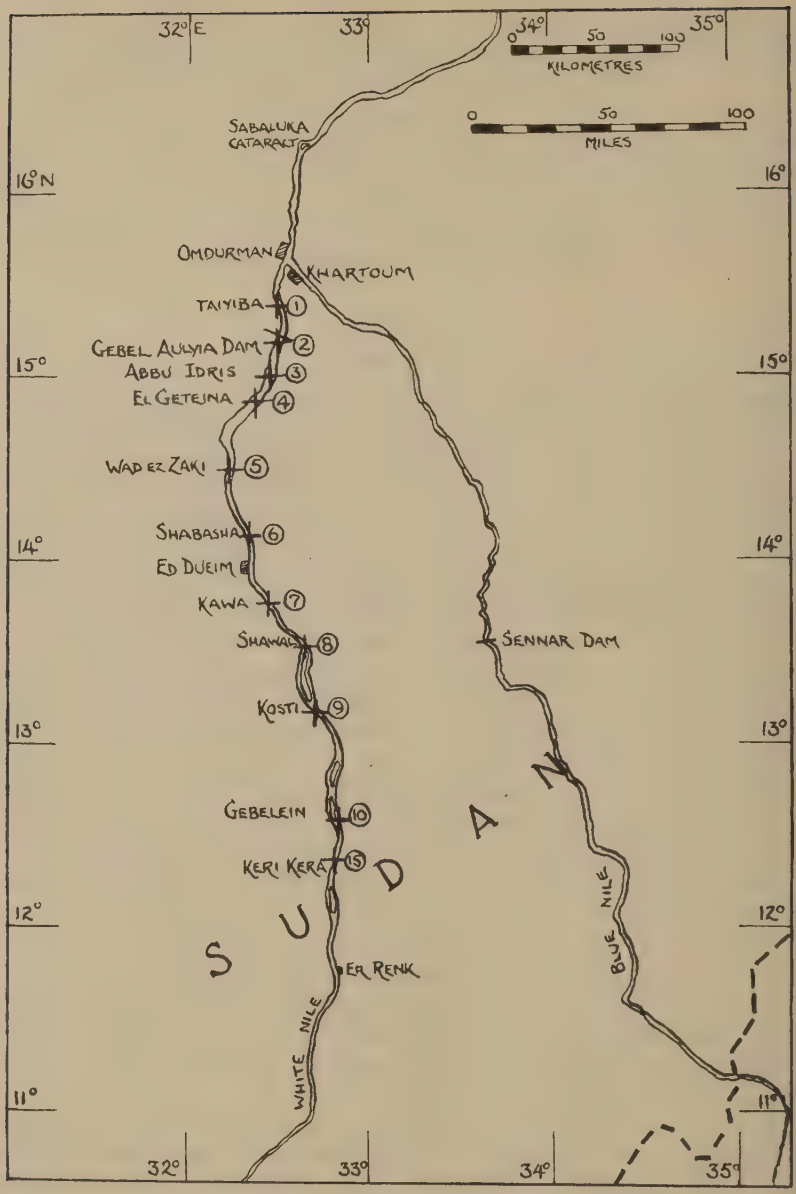

Fig. 1. Map of part of the White Nile showing sampling stations.

METHODS

Quantitative water samples were taken with a Friedinger sampler of 2 l. capacity. At each station, duplicate samples from three levels (surface, middle and bottom) were obtained except where the river was very shallow, when only surface and bottom samples were collected. The depth at which the samples were taken varied with the depth of the river. All sampling stations were in mid-stream, no account being taken of the possible variations of plankton density across the river. The position of each station is indicated in Fig. 1.

For phytoplankton studies, 250 ml. of sample were preserved with 4% formalin and stored in screw-capped jars for later examination. The density of phytoplankton was determined by transferring, with a wide-mouthed pipette, 1 ml. of well-shaken sample into a 1 ml. Naumann counting chamber. Counts were made under a $\frac{1}{2}$ in. objective of fifteen fields selected at random, two counts being made from each sample. When the density of phytoplankton was less than 500 organisms/ml., the samples were concentrated by centrifuging 10 ml. at 2000 r.p.m. for 5 min., withdrawing the upper 9 ml., and counting the phytoplankton in the 1 ml. remaining.

For zooplankton, each 2 l. sample was concentrated in the field by sieving through a nylon net with a mesh size of $20–50 \times 50–80\ \mu$. All the organisms in these samples were counted and average densities per unit volume determined for each level and station. At most stations samples were also collected with a net of the standard Windermere type, by letting the nets float downstream from the moored boat for 10–20 min. These samples were used to furnish additional information on plankton components.

Chemical and physical observations were made at each station. Water temperatures, turbidity and pH were measured in the field, while samples for later determinations of dissolved oxygen concentrations, total dissolved solids and alkalinity, were also collected.

Estimations of plankton densities are subject to technical, biological and statistical errors, and thus the smaller the sample unit the more marked will these errors be. Therefore, in drawing general conclusions, all samples taken at each station have been grouped and averaged. The results that follow express only the approximate representation of the main plankton components at the mid-stream stations indicated during the period of the investigation and do not show total production, since this was not the period of maximum productivity. Within these limits the results, nevertheless, show an unmistakable trend and a reasonable consistency.

PHYSICAL AND CHEMICAL MEASUREMENTS

(*a*) *Turbidity*

(Measured with a Secchi Disk)

It might be expected that turbidity would decrease as the influence of the dam became more pronounced, owing to the slowing down of the current and consequent settling of suspended matter. This was, however, masked by the vast production of plankton in the vicinity of the dam. Although the settling of suspended matter was observed, detritus becoming more abundant in succeeding samples taken upstream, turbidity in fact increased towards the dam.

(*b*) *Total dissolved solids*

(Measured by electrical conductivity)

The higher concentration of dissolved salts in the region of the dam (Fig. 2), may perhaps be interpreted as due to the liberation of solutes from the flooded ground.

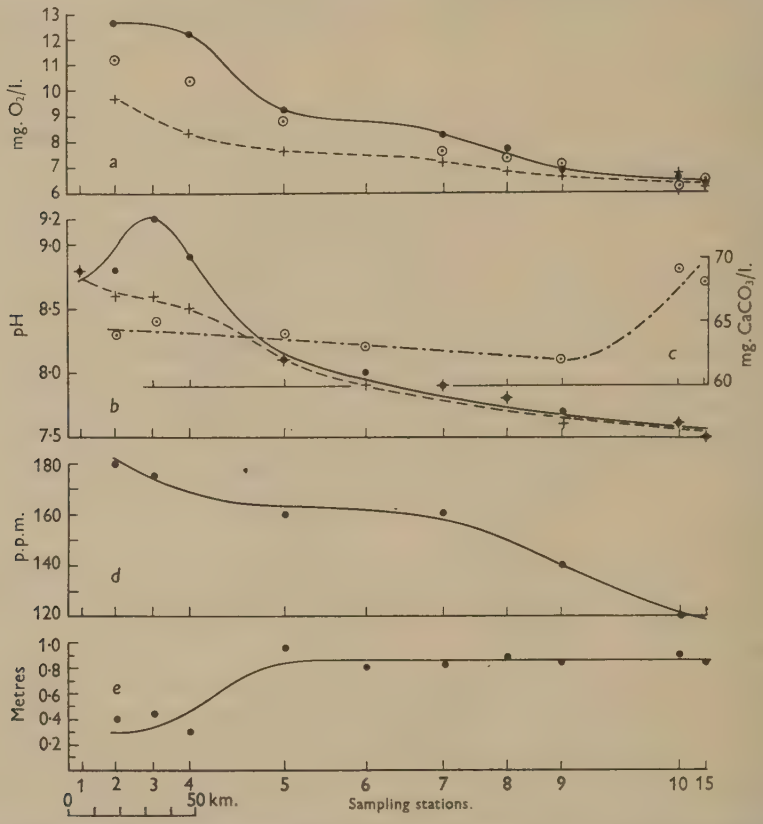

Fig. 2. Physical and chemical measurements. (*a*) Dissolved oxygen: ●—●, surface; ⊙, mid-depth; + – – +, bottom. (*b*) pH: ●—●, surface; + – – +, bottom. (*c*) Alkalinity. (*d*) Total dissolved solids. (*e*) Visibility of the Secchi disk.

(*c*) *Alkalinity and* pH

(The former estimated by titration against standard N/100 HCl; the latter colorimetrically in the field with a B.D.H. Comparator)

Alkalinity, measured as mg. $CaCO_3$/l., shows only a very slight decline between the dam and station 9, and this is followed by an increase beyond. The pH, on the other hand, shows a marked rise which cannot be accounted for by these changes in alkalinity. It seems rather to be correlated with the photosynthetic activity of the phytoplankton removing the dissolved CO_2, this being most marked in the neighbourhood of the dam (see also data for dissolved oxygen concentration). Experiments carried out on the

White Nile a few weeks before the present investigation, when the phytoplankton density was 10,000 organisms per ml. (*Anabaena flos aquae* and *Melosira granulata* dominant), revealed marked diurnal changes in pH, from about 8·0 during the night to a steady value of 9·2, attained an hour after sunrise, thus confirming the present results.

(*d*) *Dissolved oxygen concentration*

(Estimated by Winkler's method)

As with pH, it seems that the dissolved oxygen concentration can be directly correlated with the amount of phytoplankton. The relevant graph shows that not only was the O_2-concentration greatest where the phytoplankton was most abundant, but also that the differences in concentration between the upper and lower layers were greatest in these regions. Although the density of phytoplankton tended to be greater in the surface layers (Table 1), these differences were not large, and consequently it is thought that the differences in oxygen concentration are rather a reflexion of the reduction in light intensity in the lower layers caused by the dense growth of the plankton and the accompanying lessening in photosynthetic activity. This contention is supported by the differences in pH at different depths which have been recorded in these regions, the greatest values being found in the surface layers.

THE COMPOSITION OF THE PLANKTON

(*a*) *The Phytoplankton*

Observations extending over a period of three years show that the phytoplankton of the White Nile between Khartoum and the Gebel Aulyia Dam (15 km. north of station 1—see Fig. 1), is composed principally of diatoms and blue-green algae, and hence resembles that of a typical eutrophic lake. At the time of the present study, blue-green algae were dominant: samples taken on 10 December near Khartoum indicated that this group comprised 83% while diatoms formed 15% and Chlorophyceae 2% of the total population.

The dominant alga was *Anabaena flos aquae*, var. *intermedia*, forma *spiroides* Woronich, with *Lyngbya limnetica* Lemm. approaching it in importance. The principal diatom was *Melosira granulata* (E.) Ralfs, and the var. *angustissima* Müll. Also present in considerable numbers were *Anabaenopsis Cunningtonii* R. Taylor, previously recorded only from Lake Tanganyika, *A. Tanganyikae* (G. S. West) Wolosz. & Miller, *Raphidiopsis curvata* Fritsch, not previously recorded from the Nile, *Oscillatoria geminata* (Menegh.) Gom. and *O. planktonica* Wolosz. Other diatoms were *Melosira Agassizzii* Ostenf., *Synedra acus* Kg., *Nitzschia acicularis* W. Sm. and *N. palea* (Kg.) W.Sm. The Chlorophyceae were mainly represented by *Ankistrodesmus falcatus* (Corda) Ralfs, *Scenedesmus acuminatus* (Lagerh.) Chodat, *Micractinium pusillum* Fresen. and *Dictyosphaerium pulchellum* Wood. All of these algae have also been found upstream of the dam during the present investigation, though their distribution and abundance varies considerably throughout the stretch of river studied (see Table 1 and Fig. 1).

Table 1. *Density of phytoplankton at different depths at different stations*

(Figures give the number of organisms per 0·1 ml. Species and group maxima are shown in heavy type: + indicates present.)

Station ...	1			2			3			4		5			6		7			8			9			10			15		
Sampling depth (m.) ...	0	3	6	0	5	9·5	0	2	4·5	0	1·5	0	5	9·5	0	2·5	0	2	4·5	0	4·5	8·5	0	3·5	7	0	3	5·5	0	3	4·5
Melosira granulata	50	53	**65**	51	39	48	48	53	51	31	51	10	10	10	6	6	2	3	1	3	2	2	2	2	2	1	1	1	1	1	1
M. granulata, var. *angustissima*	20	**36**	10	22	24	24	34	27	22	29	15	4	5	5	3	4	2	2	2	1	1	1	1	1	1	1	2	1	1	2	3
Raphidiopsis curvata	**29**	**29**	12	10	15	7	+	5	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Anabaenopsis Cunningtonii	44	**46**	36	17	17	24	+	5	5	2	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
A. Tanganyikae	**20**	12	+	+	10	+	+	+	–	5	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Anaebana flos aquae	236	217	253	220	147	152	**310**	128	108	147	145	–	1	+	+	+	+	–	–	–	+	+	–	–	–	–	–	–	–	–	–
Anabaena spp.	22	12	20	**32**	10	12	15	15	2	2	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oscillatoria geminata	41	**50**	34	46	41	29	12	5	24	20	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
O. planktonica	**44**	22	22	32	19	32	15	7	7	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+
Lyngbya limnetica	**215**	162	154	138	150	100	46	60	53	49	65	+	1	–	1	1	–	+	–	–	–	–	+	–	+	+	–	+	+	+	+
Totals																															
Chlorophyceae*	+	+	5	+	**12**	5	5	+	3	3	–	1	+	+	2	1	1	1	1	2	2	1	1	1	1	1	1	1	+	+	+
Diatoms*	89	**114**	89	94	80	99	82	79	89	81	84	16	16	16	11	11	6	7	5	6	6	5	6	6	5	4	5	5	4	4	4
Cyanophyceae	**660**	550	530	501	410	360	420	226	203	243	240	1	2	1	1	1	1	1	+	+	+	+	1	+	+	+	+	+	1	+	1

* See p. 105 for list of principal diatoms and Chlorophyceae present.

(*b*) *The Zooplankton*

Of the zooplankton only the Crustacea have been identified specifically; the taxonomy of many tropical Entomostraca is at present unsettled and certain species or varieties here listed will be defined more clearly in the future. The Rotatoria were counted as a group while the Protozoa were not investigated because of technical difficulties. At the time of the investigation and in the region of the river studied, the following species formed the bulk of the Crustacean plankton:

Diaphanosoma excisum Sars, near but not quite identical.
Ceriodaphnia rigaudi Richard, with round and horned individuals present.
C. dubia Richard, not quite identical.
Moina dubia de Guerne & Richard, very variable.
Daphnia lumholtzi Sars.
D. barbata Weltner.
Cyclops (*Thermocyclops*) *neglectus* (Sars)
C. (*Mesocyclops*) *leuckarti aequatorialis* Kiefer, in two sizes.
Diaptomus galebi Barrois.

There is a clear distinction between the above truly planktonic forms and the adventitious species from the shore, bottom and side waters. The following additional forms have been found in the quantitative and net samples:

Arcella, *Difflugia*, *Hydridae* sp. } some of these may be truly planktonic.
Turbellaria, in bottom layers.
Cercariae of Trematodes.
Oligochaeta spp.
Urnatella (Bryozoa) fragments.
Phyllopoda: species of *Cyclestheria*, *Latonopsis*, *Pseudosida*, *Simosa*, *Pseudoalona*, *Euryalona*, *Camptocercus*, *Leydigia*, the *Alona* group, *Chydorus*, *Ilyocryptus*, *Macrothrix*, *Grimaldina*.
Copepoda: *Diaptomus processifer*, sp. of *Microcyclops*, *Paracyclops* and others.
Ephemerid nymphs, Chironomid larvae, Hydracarina.

The occurrence of these non-planktonic forms at certain stations seems to be significant and will be discussed later.

THE GENERAL DISTRIBUTION OF PLANKTON DOWNSTREAM

The densities of the main species and groups of phyto- and zooplankton at each collecting station and depth investigated are set out in Tables 1 and 2 respectively, while the total densities of phyto- and zooplankton, averaged for each station, are plotted in Fig. 3.

It is apparent that within the 352 km. from station 15 to the dam, the plankton as a whole showed a very marked numerical increase. For both plants and animals this was more than 100-fold, the river at station 15 carrying 49×10^3 algae and 0·8 animal per litre, rising to maxima of 6790×10^3 and 123 per litre respectively in the vicinity of the dam. The increase was at first slight, becoming marked at about 250 km. from the dam, but being rapid only in the final 100 km. The increase in phytoplankton continued beyond the dam, the richest sample being obtained at station 1, some 19 km. below, whilst the greatest density of zooplankton was at station 3, 19 km. above. At station 2, 1·2 km. above the dam, samples showed a marked decrease in zooplankton

Table 2. *Density of zooplankton at different depths and different stations*

(Figures give the number of organisms per litre. + Indicates organisms present at estimated density of 0·25/l.)

Station ...	1			2			3			4	5			6		7			8			9			10			15		
Depth (m.) ...	0	3	6	0	5	9·5	0	2	4·5	0*	0	5	9·5	0	2·5	0	2	4·5	0	2	8·5	0	3·5	7	0	3	5·5	0	2	4·5
Diaphanosoma excisum	2	–	3	4	–	–	5	1	4	2	1	1	1	+	1	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–
Ceriodaphnia rigaudii	44	6	30	54	3	8	105	17	37	17	5	2	7	3	1	1	1	1	+	+	–	–	–	–	–	–	–	–	–	–
C. dubia	1	–	–	1	–	1	1	+	1	+	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Moina dubia	–	–	1	1	–	+	1	+	+	1	+	1	+	1	1	+	+	–	1	–	+	–	–	–	–	–	–	–	–	–	–
Daphnia lumholtzi	–	–	–	1	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
D. barbata	–	–	–	–	–	–	–	+	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Thermocyclops neglectus, female	–	–	1	4	1	1	2	–	1	1	+	–	–	1	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
T. neglectus, male	1	–	1	1	–	–	2	–	+	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Mesocyclops leuckarti aequatorialis, female	–	–	–	1	–	–	1	–	1	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. leuckarti aequatorialis, male	–	–	–	1	–	+	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyclopidae, juvenile	5	1	4	4	–	1	4	1	3	4	1	1	1	1	1	–	–	–	1	+	–	+	–	–	–	–	–	1	+	–
Cyclopidae, nauplii	30	14	45	16	5	10	58	12	22	12	6	5	8	5	3	1	+	1	1	1	+	+	1	+	1	+	1	–	+	–
Diaptomus galebi, female	–	–	1	2	–	–	1	–	+	–	1	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–
D. galebi, male	–	1	–	4	–	–	1	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
D. galebi, juvenile	2	1	4	11	–	–	5	2	2	3	1	+	+	–	1	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
D. galebi, nauplii	9	1	9	2	1	2	7	1	2	3	1	1	1	2	1	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Rotatoria	17	10	13	6	5	5	47	12	12	10	7	2	4	12	3	4	5	3	6	–	–	+	–	–	–	–	–	–	–	–
Adventitious forms	–	–	1	–	–	1	–	–	1	–	–	–	–	–	–	+	–	–	–	–	1	–	–	2	–	1	+	+	+	+
Total population	110	32	111	109	16	30	241	46	87	52	23	13	23	25	11	7	7	6	9	1	1	1	1	2	1	1	1	1	1	+
Average population at each station	84			52			125			52	20			18		7			4			1			1			1		

* Samples from 1·5 m. at station 4 were lost.

which may have been due to the increase in current near the dam's sluices; this tends to be confirmed by the reappearance here of adventitious forms. Since two of the samples from this station were lost, too much weight cannot be attached to this observation. Two other sets of samples from station 2, one taken shortly before and the other shortly after the present investigation, showed plankton densities of 73/l. on 8 December and 103/l. on 29 December 1951. All three samples thus show a decrease, compared with the 123 organisms/l. at station 3. In the graph (Fig. 3), all three figures have been plotted and the graph drawn through the average (73·8) of these densities.

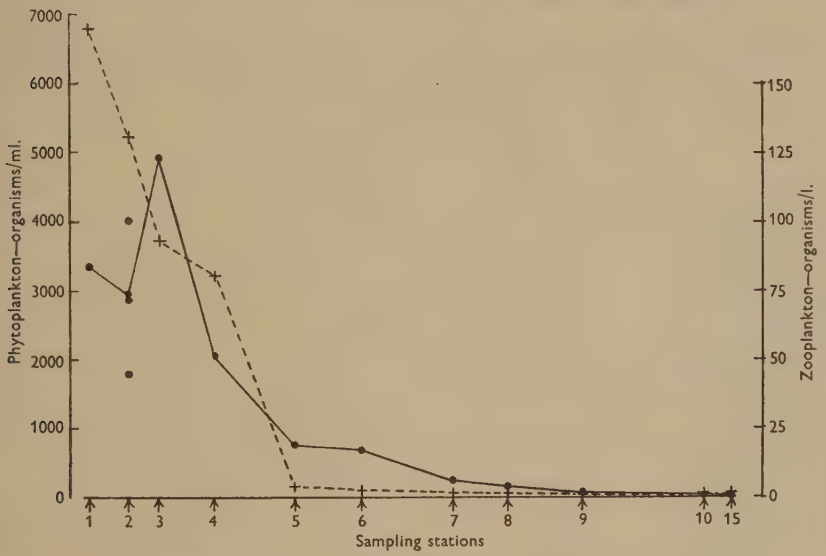

Fig. 3. Average density of phytoplankton (+ – – +) and zooplankton (●—●).

THE DISTRIBUTION OF THE PLANKTON COMPONENTS AND THE LOCAL DIFFERENTIATION OF THE PLANKTON

The results considered above are based on the total density of plankton at each station. The role which each plankton component plays in the downstream and vertical distribution will now be considered.

(*a*) *The Phytoplankton* (Table 1)

Consideration of Table 1 shows that all species reached their maximum development in the three stations (2, 3 and 4) nearest the dam, though many of them continued to multiply for some miles below it. This may be due to the mixing and better aeration of the water as it passes through the sluices. That such mixing does take place seems to be indicated by the vertical distribution of several of the more abundant species. Between stations 15 to 5, where the phytoplankton is scarce and river-like conditions apparently predominate (Fig. 1), the distribution in depth seems to be a random one. Downstream of station 5, many species show a tendency to reach their greatest density at the surface and in the middle depths, and at stations 1 to 4, all total

maxima occurred at these depths. It is clear from Table 1 that the dominant group of algae, the Cyanophyceae, showed a tendency to assemble near the surface in the lake-like stretch (stations 2–5), though diatoms appeared to remain evenly distributed. Station maxima of the commonest species (> 300/ml.) of Cyanophyceae at stations 2–4 also tended to be at the surface, but at station 1, where the 'lake' has reverted to river, two species (*Oscillatoria planktonica* and *Lyngbya limnetica*) had maxima at the surface, two (*Anabaenopsis Cunningtonii* and *Oscillatoria geminata*) in the middle layers, and the dominant *Anabaena flos aquae* at the bottom, suggesting some mixing of the plankton as water passes beyond the dam.

Table 3. *Maximal appearance of certain zooplankton components in single samples and at single levels and stations, arranged according to abundance*

	Sample maximum			Level maximum			Station maximum	
	No. per litre	Level (m.)	Station	No. per litre	Level (m.)	Station	No. per litre	Station
Ceriodaphnia rigaudi	117·0	0	3	104·5	0	3	52·5	3
Cyclopidae, nauplii	70·0	0	3	57·7	0	3	30·6	3
Rotatoria (total)	53·5	0	3	46·2	0	3	23·5	3
Diaptomus, nauplii	9·0	0	1	6·5	0	3	6·1	1
Diaptomus, juvenile	10·5	0	2	5·0	0	3	2·8	3
Cyclopidae, juvenile	5·0	0	1	3·8	0	3	3·8	4
Diaphanosoma	5·0	0	3	4·7	0	3	3·3	3
Diaptomus galebi, male	4·0	0	2	0·8	0	4	1·0	2
Thermocyclops neglectus, female	3·5	0	2	2·0	0	3	1·4	2
T. neglectus, male	2·5	0	3	2·3	0	3	0·8	3
Moina dubia	2·5	0	3	1·3	0	3	0·8	4
Diaptomus galebi, female	1·5	0	2	1·5	0	3	0·4	2
Ceriodaphnia dubia	2·0	9·5	2	1·3	9·5	2	0·9	2
Mesocyclops leuckarti aequatorialis, female	1·5	0	3	1·3	0	3	0·6	3
Daphnia barbata	1·0	4·5	3	0·8	4·5	3	0·3	3
Mesocyclops leuckarti aequatorialis, male	1·0	0	4	0·8	0	3 and 4	0·8*	4
Daphnia lumholtzi	0·5	5·0 4·5	2 3	0·5	4·5	3	0·3	2

* Only one level at this station.

(*b*) *The Zooplankton* (Table 2)

All species of Cladocera were represented by a majority of parthogenetic females; further inquiry into the sexual processes has been left to the future. In the Copepoda, sexes and stages were counted separately; juvenile forms of Cyclopidae counted together; Rotatoria were treated as a whole; similarly non-planktonic (adventitious) forms.

Each species, and each group of animals, shows a gradual increase towards the dam; or upstream, a thinning out which leads to the disappearance of some species from the quantitative samples. In the typical river stations from 9 upstream juvenile *Cyclops* and Rotatoria, besides adventitious forms, were alone sufficiently numerous to appear in the volumes of water examined (12 l. at each station). At such places, net samples clearly afford a more accurate picture of the plankton's composition.

Quantitative data have been assembled in Table 3 to give details of the maximal appearance of certain components arranged to show the maximal occurrence in any one sample (sample maximum), in all samples from one level at each station (level

maximum), and in all samples from all levels at each station (station maximum). This table shows that all the seventeen plankton components have their maximum concentration in the four stations nearest the dam, showing, as in the case of the phytoplankton, that the greatest development takes place in the last 50 km. above the dam, though data from station 1 indicate that the increase of some species may persist for some miles below it. Sample and level maxima show considerable differences, which suggest that even in a limited space, the horizontal distribution is uneven and that a representative picture of the fauna cannot be gained from single 2 l. samples. Sample and level maxima occur mainly at the surface, except for *Ceriodaphnia dubia*, *Daphnia lumholtzi*, and *D. barbata*, but for which the data are too scanty to draw any conclusions.

Table 4. *Percentage occurrence of zooplankton species at station 3, quantitative and net samples compared*

	Quantitative samples	Net samples
Cladocera		
Diaphanosoma excisum	4·9	3·7
Ceriodaphnia rigaudi	79·4	79·7
C. dubia	1·08	1·0
Moina dubia	0·88	1·0
Daphnia lumholtzi	0·25	—
D. barbata	0·51	0·3
Total	87·0	85·7
Copepoda		
Thermocyclops neglectus, female	1·38	1·7
T. neglectus, male	1·26	0·3
Mesocyclops leuckarti aequatorialis, female	0·76	0·3
M. leuckarti aequatorialis, male	0·37	—
Cyclops, juvenile	3·5	1·0
Diaptomus galebi, female	0·5	1·7
D. galebi, male	0·63	3·3
D. galebi, juvenile	4·78	6·0
Total	12·75	14·3

Data on the vertical distribution of the zooplankton can also be gleaned from the total population numbers in Table 2. Although the material is scanty, a few conclusions seem to be justified. Surface samples are richest at stations 2, 3, 6 and 8, while bottom and surface samples were equally rich at 1 and 5. Middle layers were least populated in 1, 2, 3 and 5, whilst the differences in vertical distribution are insignificant in the true river stations, i.e. 7, 9, 10 and 15. It would seem that under normal river conditions, outside the influence of the dam, there is little stratification. The more lake-like the conditions become, however, the more the ever-increasing plankton population is differentiated into strata.

There is an appreciable difference in the value of quantitative data for the phytoplankton and for the zooplankton, for the former is always present in measurable amount while the latter diminishes to such a degree upstream that it cannot be estimated even in a series of 12 l. samples. Net samples have therefore been used to provide additional information about the occurrence of the zooplankton components. In each net sample 3×100 specimens were counted, excluding nauplii and Rotatoria,

which are only partly caught. The percentage occurrence of the fourteen pure plankton components in the net plankton was compared with their occurrence in the quantitative samples, calculated anew with the omission of nauplii and Rotatoria. Table 4 shows for station 3 the similarity in percentage occurrence in quantitative as compared with net samples.

Similar calculations and comparisons, made for all stations for which sufficient material was available, afforded results comparable to those given above. In Table 5 only the total percentage occurrence of Cladocera, Copepoda and adventitious forms in quantitative and net samples is given for each station. There are considerable differences between quantitative and net samples in the case of the adventitious forms. This is because net hauls were taken from the surface, whilst adventitious forms are usually more plentiful in the deeper layers. Nevertheless, it seems possible to trace a trend in the representation of the zooplankton components. The net samples also amplify the picture of the zooplankton in the upper stretches of the river. They show

Table 5. *Total percentage occurrences of zooplankton by groups*

*=no net sample taken; + =less than 0·5% occurrence.

	Cladocera		Copepoda		Adventitious	
Station	Quant.	Net	Quant.	Net	Quant.	Net
1	81	*	18	*	1	*
2	72	74	26	26	2	+
3	87	86	13	14	+	+
4	68	*	32	*	—	*
5	80	87	20	13	—	+
6	60	75	40	25	—	—
7	60	67	35	31	5	1
8	36	68	43	30	21	2
9		26		61		14
10	5	29	32	47	64	25
15		14		64		23

Because of the small numbers of organisms present the quantitative samples for stations 9, 10 and 15 have been grouped and averaged.

that the disappearance of certain components in the quantitative samples from upstream is only due to their diminution, since only *Ceriodaphnia dubia* and the two *Daphnia* species disappear from the net samples of the true river stations (9, 10 and 15), whereas all the others were recorded, though in very small numbers.

From Tables 1 and 5 it is now possible to trace the distribution of the main components of the plankton, and reconstruct a picture of the gradual changes in its composition. In the region farthest from the dam the plankton consists of a sparse community of plants and animals, including truly planktonic, along with bottom- and shore-inhabiting species. These are carried downstream in the turbulent water, rich in detritus and dark in colour. Of the plants, diatoms (principally *Melosira granulata*) constitute 75–90% of the population, with Chlorophyceae (mainly *Ankistrodesmus falcatus* and *Scenedesmus* spp.) next in importance (8–21%), a sparse population of Cyanophyceae (about 5%) and a few dislodged epiphytic algae. Associated with these is a zooplankton of Copepoda (32–63%) and Cladocera (5–29%), along with

a considerable proportion of adventitious forms, comprising 14–24% and in places rising to 60% of the whole population.

This mixed community, in part truly planktonic, is carried downstream until, apparently at about 240 km. from the dam, it becomes noticeably affected by changes in hydrological conditions. Detritus and adventitious forms settle out and the water becomes conspicuously cleaner. As lake-like conditions develop, the true planktonts find their particular requirements and begin to multiply rapidly. Not only does the density of the plankton increase, but its composition changes. For the zooplankton the crucial turning point is between stations 8 and 9. Up to there Copepoda are dominant, but between station 7 and the dam Cladocera (60–87%) dominate the Crustacean plankton, while Copepods show a relative decrease (12–40%). Adventitious forms disappear altogether in this region, though they reappear near the sluices of the dam, presumably being swept into the plankton with the increased flow of water. The turning point for the phytoplankton is much nearer the dam, the marked change in the relative importance of its constituents accompanying the vast increase in productivity between stations 5 and 4. Diatoms, which are dominant in the upper reaches, decrease from 93 to 31%, while Cyanophyceae become the dominant group, increasing from 5 to 86% of the total population. Nevertheless, all three groups increase numerically as the dam is approached and continue to increase beyond it.

Previous workers have noted that the quality and quantity of the zooplankton may be closely related to the nature of the phytoplankton. Lèfevre (1948), for example, describes changes from a rich to a poor zooplankton which were associated with a change from a chlorophycean to a cyanophycean phytoplankton. The vast development of Cyanophyceae in the plankton near the dam may thus have been an additional factor causing the decline in zooplankton at station 2. Although the biological effects of impounding water by dams have been previously observed, notably by American authors, it seems premature at this stage to compare the present results from one short period of observations, with those gained elsewhere. As far as can be ascertained, however, no quantitative data from any African river, or indeed from any large tropical river, have been published. Consequently, the present paper is regarded merely as fact finding and only a contribution to the extensive study of Nile biology which is in progress.

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SUMMARY

1. The biological effects of impounding water by a dam have been investigated on the White Nile, by taking a series of plankton samples from the Gebel Aulyia Dam upstream for 352 km.

2. From the sampling station farthest from the dam to the dam itself, the plankton showed a numerical increase of more than 100-fold, the phytoplankton rising from 49 to 6790×10^3 and the zooplankton from 0·8 to 123 organisms per litre. This increase

has been related to the changes from river to lake-like conditions. The maximum density of both phyto- and zooplankton was attained in the last 50 km. above the dam.

3. Changes in the composition of the plankton were also observed. In the upper regions it was mixed with non-planktonic forms, whilst of the truly plankton forms, diatoms and copepods predominated. With increasingly lake-like conditions the adventitious forms disappeared and Cyanophyceae and Cladocera gained dominance.

4. Some physical and chemical factors were investigated. Although there was a loss of suspended detritus, turbidity increased owing to the vast development of phytoplankton near the dam. The dissolved oxygen concentration and the pH also showed marked increases, which have also been correlated with the rich phytoplankton near the dam.

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A CONTRIBUTION TO THE STUDY OF THE ECOLOGY OF CORIXIDAE (HEMIPT.)

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(With 1 Figure in the Text)

The family Corixidae is a particularly attractive one to ecologists because, though most of the thirty-two British species are common and widely distributed, every one has a restricted habitat and there is none that can be called 'the common *Corixa*'; none that is comparable with *Limnaea pereger* among Mollusca for example. A considerable amount of work on the ecology of the group has been done during the last 25 years, but nearly all of it has been of a purely descriptive nature, collections being made and then features common to every place where a given species occurred being sought. Sutton (1951) has investigated the feeding, but otherwise rather little attention has been paid to these and other habits which must be studied before the work can be taken beyond the preliminary descriptive stage.

This contribution is another descriptive study, based on records from two sources: first a series of the author's, comprising a few from the Lake District that have not been analysed before and a number from other parts of the country made on such occasions as excursions of scientific societies and holidays, and including some kindly sent by friends. The second is the records published by various authors collaborating in a scheme originally started by Dr G. A. Walton, and some manuscript notes that I received from Dr H. D. Slack. Their names are set out in Table 2, and they are referred to henceforth in the text as 'the other authors'. The disadvantage of miscellaneous records is that during a brief single visit it is often not possible to note all the features of a place that should be noted; over 10% of the writer's records were discarded because they were not complete enough. Their advantage is that, coming from many parts of the country, they correct wrong notions arising from close study of a small area. It is hoped that, since the present contribution is based almost entirely on data of this kind, it will have interest on account of the light it throws on the value of miscellaneous records.

The analysis of the author's records takes the form of arranging the collecting stations in groups according to the species of corixid found in them and then looking for features common to each group. It has not been possible to analyse the other records in the same way because not enough are sufficiently complete; many give no indication of the relative abundance of the various species and some of the rest do not give an account for each station of all the features that appear to be important in the ecology of the Corixidae. These records have, however, the merit of being numerous, and the mathematical treatment which they therefore demand has been attempted.

Definitions and the correct use of such words as lake and pond provide an immediate difficulty in a study of this kind, and lead to the question of whether satisfactory

categories will ever be found. The author's belief is that they will not. Obviously between two extremes there will be every grade of intermediate and any divisions must be arbitrary. In the author's experience satisfactory criteria can often be found as long as only one group of animals or plants is being studied, but, when two or more are compared, it is rarely that the dividing places that each provides coincide, and therefore no general scheme is possible. Accordingly, no scientific application of names has been attempted here and local usage has been followed. A lake is obviously large, and a pond smaller, but it is impossible to give a definite area above which the term 'lake' and below which the term 'pond' should be applied to a body of water. In general, the shores of ponds are not appreciably eroded by wave action and those of lakes are. Under the name pond are included here the quite small farm ponds and field ponds that usually have no flow through them and have been dug out of an impermeable soil to provide water for cattle. Fishponds are larger and deeper and usually have an inflow and an outflow. In the Lake District a fishpond becomes a tarn and in Scotland a lochan and such places are rarely less than 2 m. deep. In contrast is the peat pool which, though usually small, may be a hectare ($2\frac{1}{2}$ acres) or more in extent, but which is usually less than one metre deep and without perennial inflow and outflow.

THE AUTHOR'S MISCELLANEOUS COLLECTIONS

The catches are set out in Table 7, the figures being numbers caught in a pond-net not wielded in a standard way at each place. The collecting stations have been arranged according to the species found in them in five groups, some of which are subdivided. At every station in a group one species, or one of several species that are often found together, is common, usually the commonest species, though sometimes more weight has been given to a combination of species than to total numbers. A few stations that might have fallen equally well into either of two groups have been assigned to one on physiographical features, and some of the subgroups have been delimited entirely in this way. Furthermore, physiographical considerations seem to justify setting the boundary between groups IV and V in the middle and not at the end of places where *C. nigrolineata* is the characteristic species. When possible one group or subgroup leads on to another through species common to both, but a trend may diverge, and since this cannot be shown in a two-dimensional table, the two diverging groups must be placed one after the other and a break in the continuity made.

Group I. Corixa lacustris*, C. falleni *and* C. concinna

Eleven of the stations are in rivers, two in large ditches, and eleven in lakes. In no other group except group III are there any water-bodies of these kinds. Since *C. punctata* is the commonest species at the remaining station, it might have been placed in group V, where as it is small enough to be called a pond it would have been among places physiographically similar. It is a station that links the two, and has been allocated to group I because all three of the species characterizing that group are fairly abundant in it. Group I then, except for this last place, includes the places where the bottom is swept by current or subject to the action of waves. That *C. lacus-*

* Hitherto known by the name *C. striata* (see Macan, in press).

tris should be the most abundant and most often found species is not surprising from what is known already about it (Brown 1943, pp. 218, 219; 1948, p. 188; Macan 1938). *C. falleni*, the only other species present in big numbers, occurs at fewer stations. It is abundant only in the lakes (I *d*), all of which incidentally are calcareous; it occurs in all the stations of subgroup *c* which comprises calcareous rivers and ditches, but less often in the soft-water rivers of subgroup *b*; it is absent from subgroup *a*, two rivers swift enought to have a stony bottom, though one of them is calcareous. Brown (1948, p. 192) and Walton (1943, p. 251) have shown that *C. falleni* is a calciphile, and evidently it is not as tolerant of exposure as *C. lacustris*, but its habitat has not been described completely, and there are stations at which either its absence or its complete predominance over *C. lacustris* are not explicable. In Blelham Tarn, a Lake District lake, Macan (1949) found it rather unexpectedly in thick vegetation, though it was numerous only near the mouths of streams. In the Danish lakes (Macan, in press) it

Table 1. *Analyses of some lake waters*

		Oxygen absorbed from $KMnO_4$	Conductivity $K_{18°} \times 10^{-6}$	Alkalinity ($CaCO_3$ equiv. mg./l.)	Nitrate (mg./l.)
Loch Rannoch (unproductive, soft-water, rocky lake)	Inflow	12·7	22	3·3	—
	Outflow	6·8	31	5·5	—
Windermere (fairly productive soft-water lake)		1·4	49	8·7	0·8
Loch Leven (productive, lowland hard-water lake)	Inflow	4·7	164	75	11·5
	Outflow	7·6	118	43	1·9
Loch Gelly	Outflow	7·6	242	70	10·0

was frequently encountered, but was never abundant on exposed sandy shores or in reed-beds, and only occurred in numbers in an artificial bay in a reed-bed and in a muddy ditch flowing into a lake. It seemed to be associated with conditions which, though somewhat exposed, nevertheless permitted the settling of organic debris on the bottom.

Penmon Priory pond has some flow through it but not enough to affect the bottom, which is made up of dead leaves representing probably the accumulation of centuries. The abundance of *C. lacustris* and *C. falleni* in such a place is difficult to explain. The other authors record both species in large bodies of water and in running water but also took large numbers in a few ponds. It is not possible to make out with certainty from their descriptions any features common to all these ponds, and further investigation of small bodies of water containing *C. lacustris* and *C. falleni* should be interesting. It is noteworthy that both Brown (1951) and Popham (1951) have brought forward evidence that these two fly less than other species.

C. concinna, the third species characteristic of group I, is uncommon, and is recorded in abundance only twice by the other authors and at but two of the stations under review. One of these was the pond at Penmon Priory, discussed above, and the other, quite different, was Loch Gelly which is about a quarter of a mile square and lies in the coalfield area north of Edinburgh. Two collections were made, one on a sandy bottom where there was no vegetation, the other in a narrow zone of *Iris* at the lake's

edge. Dr Mortimer kindly analysed a sample of water and his results are set out in Table 1, together with some others for comparison. Loch Gelly has an unusually high concentration of dissolved salts. *C. concinna* occurs at 10 of the 117 places from which the present collections were made, and four of these are in group I. Association with *C. lacustris* has been calculated by means of the χ^2 test, using the ordinary fourfold table with number of stations with both species, number with neither, and numbers with each one without the other. χ^2 is 6·2 which is highly significant. Five of the ten occurrences are in ponds in group V and the association of *C. concinna* with *C. lateralis* is also highly significant. Two of the ponds were polluted by animal dung and two were in salt marshes. The connexion between polluted and saline localities is discussed later.

Walton (1943) records *C. concinna* abundantly from Blagdon Reservoir, which is calcareous and without much vegetation or vegetable remains, and Pearce & Walton (1939) found great numbers in 'SH 14. Pond by roadside at Warren Farm, St Leonards-on-Solent'. This place is evidently near the sea and might therefore be saline, and near a farm and might therefore be polluted, but there is no evidence that it is either, and the record does little more than illustrate the tantalizing nature of other people's records. Neither Brown nor Popham found more than a few *C. concinna*. There is then a suggestion that this rare corixid, though not a salt-marsh species, is often associated with salinity above the average for inland waters, but more than that cannot be said.

Two other species that occur fairly often in group I are *C. distincta* and *C. fossarum*, which is to be expected since Macan (1938) has shown that they are associated with *C. lacustris* in Windermere and replace it as vegetable organic matter accumulates on the bottom. *C. sahlbergi*, *C. praeusta* and *C. punctata* link group I with groups II, III and V respectively.

Group II. C. sahlbergi

Scarcity of other species is another characteristic of this group. All the places are small and floored by vegetable remains. The first and last are fen pools. Hutchinson (1926) records *C. sahlbergi* in pools in Wicken Fen, Walton (1943) in overgrown ditches in the fen country of north Somerset. The second place is a woodland pond with the bottom covered with dead leaves, and this is another well-known association to which Macan (1938, p. 15) and Walton (1943, p. 254) have previously drawn attention. The remaining two records are from Lake District mosses occupying former lake basins, which probably did pass through a fen stage but which are now covered by bog, so that *C. scotti* and *C. castanea*, rather than *C. sahlbergi*, are to be expected. Unfortunately no water analyses, which might have explained this apparent anomaly, were made.

C. sahlbergi is found almost wherever there are large quantities of decaying vegetable matter. It is typically a species of stagnant places and usually small places, but it may occur in others. The records from the River Misbourne (group I *a*) are interesting in this connexion, this being a fairly swift river flowing over a gravelly bed in which the only harbourage for creatures such as corixids was provided by small patches of *Ranunculus aquatilis*. Organic debris settled in these patches. Though only one is quoted, four collections, all large, were made and *Corixa sahlbergi* was found in each of them.

Group III. C. praeusta*

There are physiographical similarities between groups I and III, as has been noted, and faunistically they resemble each other apart from the predominance in group III of *C. praeusta*. Some clue to the reason for this emerges from an examination of the two rivers, which are the only rivers outside group I. Of the River Cree it is not possible to speak with certainty, because no analysis was made, but it did seem likely that fouling of the water's edge by cattle produced at least a local effect. About the River Blackwater, on the other hand, there is no doubt; it was obviously polluted by an overloaded sewage works. None of the other places were polluted and it is therefore appropriate to digress at this point to see what published records there are of any relation between sewage and *C. praeusta*. Teyrovsky (1952) noted that the proportion of it was highest in the most, and lowest in the least, polluted of three ponds in Poland. Macan (1938, table 6) took only this species in High Man Tarn, which, when the collection was made, was of a pea-soup colour owing to fouling by a big population of ducks that was being reared on it. Lindeth Tarn, in the same table, had a poultry farm on the slopes beside it. Macan postulated an association of *C. praeusta* with dead leaves as well as with organic matter of animal origin. There is, therefore, some connexion between pollution and the presence of *C. praeusta*, but, as is noted by all the other authors, the characteristic species of water polluted with animal excrement is *C. lateralis*, which is rarely found with *C. praeusta* and shows no association with it when the χ^2 test is applied. *C. lateralis*, however, is rarely found except in quite small bodies of water, whereas *C. praeusta* is generally taken in bigger ones, and it can only be surmised therefore that pollution of a large body of water with some flow through, and pollution of a small stagnant pond produce conditions that differ in some fundamental way. It might be expected from the conclusion reached above about it that *C. concinna* would prove to be associated with *C. praeusta*, but the χ^2 test shows that it is not. *C. concinna*, however, inhabits open sandy bottoms whereas *C. praeusta* is generally found where there are more vegetable remains, and the two may bear to one another the same relationship as *C. lacustris* does to *C. distincta* and *C. fossarum*. The likelihood of this is strengthened by the observation already made that *C. concinna* is associated with *C. lacustris*, while a glance at Table 7 shows that *C. praeusta* is frequently found with *C. fossarum* and *C. distincta*. The idea is also supported by the data that Walton (1943) gives in his fig. 15 on p. 274.

Reverting now to Table 7, Butterby Marsh is a dead loop of the River Wear, completely cut off but stated to have a fair water-table flow. It drains good agricultural land and contains much vegetation. The pond at Birmingham was similar. Helton Lake is now little more than a bulge in a river which, on the east side, drains calcareous limestone, and *Phragmites* beds are continuous. On the east side the reeds fringe a big area of fen that has evidently once been part of the lake, but on the other meadow. *C. praeusta* is found all over the lake but is abundant only along the edge of the meadow; it was numerous at each of three stations thus located and not at any of fourteen elsewhere in the lake.

* Two places with a sparse fauna in which *Cymatia coleoptrata* (see footnote to Table 7) predominated are included because they appear to fit in here better than anywhere else.

Llyn Hendref and Llyn Coron in group I both contained *C. praeusta* and both are calcareous lakes surrounded by agricultural land. Llyn Coron, the larger, is about half a mile long and a little less in breadth. Macan (1938, 1949, in press) did not find *C. praeusta* abundantly in any of the Lake District lakes except Blelham, which is by far the smallest and not as large as Llyn Coron, nor in lakes in Denmark, which suggests that size has some significance; *C. praeusta* is rarely found on the one hand in the large lake and on the other in the small stagnant pond. In sluggish rivers, large ponds with flow through them, and small lakes, it is associated with eutrophic conditions which may be due either to organic matter from an external source such as animal excrement or dead leaves or to copious production in the lake itself due to a rich supply of plant nutrients washed in from well tilled land around. It is also, with *C. fossarum* and *C. distincta*, a species of sheltered places where organic matter has been able to accumulate on the bottom.

The other two places where *C. praeusta* was abundant are of a different kind and reveal an aspect of its behaviour that is important in ecological studies. Headley's Tarn when first visited had only just been made, and Rulbut's Tarn, though possibly it had never been completely dry, had evidently from the land vegetation that covered the shallow parts undergone a considerable rise in level just recently. Brown (1943, p. 225; 1951, p. 542), Popham (1949, p. 42; 1951, p. 272) and Macan (1938, p. 16) have all noted that this species takes wing readily and is one of the first invaders of new places.

Group IV. C. scotti, C. castanea, C. semistriata, C. venusta, C. germari, C. wollastoni, C. nigrolineata

This group, subdivided into five, is characterized by more species than any other and by physiographical uniformity. Almost all the stations are situated in peaty surroundings on heaths, moorlands or mountains, have an oligotrophic or dystrophic nature, and are small. *C. distincta*, *C. praeusta* and *C. sahlbergi* provide some slight link with the foregoing groups, but most of the species that have been important up to now hardly appear at all. In IV *a–c*, *C. scotti* and *C. castanea* are abundant at some or all of the stations. The habitats of these two species are well known (Macan 1938; Walton 1943); they occur in base-deficient places, *C. scotti* on an open bottom that may be of sand or of peat, *C. castanea* in thick vegetation. Accordingly, when an attempt to arrange the stations in group IV in sequence with one species leading on to another was made, it was felt that these were the two species that could be ignored; in other words, when the impossibility of arranging a complex scheme on the two dimensions of a piece of paper manifested itself, *C. scotti* and *C. castanea* were the species to be sacrificed.

Interest in IV *a* centres round *C. semistriata*. Moine Mohr 2 was a pool formed by turf-cutting in peat bog, but as it was near the sea the water was probably not base-deficient. The next locality was beside a calcareous marl lake in a fen intersected by ditches which broadened out into pools occasionally. Gormer Lake was a heathland pond in Berkshire and apparently a typical *scotti–castanea* locality apart from some enrichment by dead leaves. The last place was a moorland pool that may have been temporary. Hutchinson (1926, p. 248) records *C. semistriata* in shallow turf cuttings

in the alkaline peat of Wicken Fen. Walton (1943, p. 256) writes that in North Somerset, which is also a region of alkaline peat: '*C. semistriata* occurs in abundance only on the lowland peat moors' and later on he mentions that it is dominant in peat cuttings. Popham (1949, p. 42) found it 'most abundantly in moorland habitats with little vegetation or with the bottom lined with *Sphagnum*' but, as he took only fifteen specimens altogether in six places (p. 6), it can hardly be said to have been abundant anywhere. Brown (1943, 1948) also took only a few specimens. *Corixa semistriata* appears to be a species of small and shallow collections of water, mainly in alkaline peat though its range may extend to acid places where it meets *C. scotti* and *C. castanea*. That it is not more closely associated with *C. sahlbergi* suggests that it haunts open rather than overgrown places.

The places in IV*b*—two heath ponds in southern England, a moorland pond in Wales, a peat pool in Cornwall, and two larger bodies of water in the mountains in Scotland—all provide typical *C. scotti* and *C. castanea* habitats. Rhos Hirwaen is a clay-capped area, once calcareous but now deficient in lime and other salts to a depth of 2 ft. owing to leaching. An old artificial pond held water. Unfortunately there was no opportunity to analyse it, but the vegetation suggested acid conditions, and it appeared a typical haunt of *C. castanea*. It was, therefore, interesting to find *C. sahlbergi* as well—an indication possibly of some amelioration of the austere conditions by calcium from the lower layers of the soil.

The places in IV*c* contain *C. venusta*, all but the last, which has a fauna that links it with subgroup *d* in which it might equally well be. Of the eleven places in which *C. venusta* was taken, seven are small streams or ditches, one is a high pool, two are ponds, and one is a quarry pond. In Lochan Lairig *C. venusta* was found only on or near deltas. This species is a well-known inhabitant of running water, usually small steams draining poor land, and Brown (1943, p. 227) confirms Walton's observation that it tends to occur in running water at low altitudes but in pools higher up. In these high pools it is usually not numerous. These two and other authors also found *C. venusta* in ponds, but whether it is often associated with deltas in such places, as might be expected, cannot be ascertained from the records. Macan (1938, p. 16), Popham (1949, p. 6) and Pearce & Walton (1939, p. 161) record fair numbers in quarry ponds, the first two mentioning that the ponds were floored with rock or stone; *C. venusta* seems, therefore, to be the chief species of such places as long as the original bottom remains uncovered by accumulating organic matter. In larger places the corresponding species is *C. lacustris*. The occurrence of both seems to be related not only to the nature of the bottom but also to flow, for, though generally confined to an inorganic substratum in still water, they may be found on an organic one in running water. Waterston Moss, for example, is a cut through peat.

In IV*d*, again with the exception of a last connecting-link station, one species, in this case *C. germari*, is usually abundant and always the commonest. All the places are surrounded by peat. The pH of Great Rundale Tarn was less than 5, its alkalinity nil, and calcium 1·45 mg./l. Brackenber Tarn was another typical base-poor moorland pond, though conditions in it were not quite as extreme, the alkalinity being the equivalent of 2·3 mg. $CaCO_3$/l. and the calcium concentration 5·5 mg./l. Loch Kinardochy gave the unexpectedly high readings of 34 mg. $CaCO_3$/l. in the inflow and

25 mg. $CaCO_3$/l. in the outflow. Moine Mohr 1, which lay near the sea, was not analysed. It was about 1000 m.^{2} in area, and the rest were somewhat larger but none was more than about a metre deep. This combination of a relatively large size and a shallow uniform depth was peculiar to the places in subgroup IV *d*. Walton's (1943, p. 274) record of *C. germari* in the calcareous Blagdon reservoir affords a striking contrast. The author has recently found it abundantly in calcareous loughs in Ireland.

Glaenocorisa propinqua occurred in all four places and nowhere else. Walton (1943, pp. 250 and 271) records that it is abundant in the open water of Priddy Pool in north Somerset and gives place to *Corixa scotti* and *C. castanea* in the shallows. This is the only record of *Glaenocorisa propinqua* occurring abundantly known to me, apart from one of my own from a big open concrete reservoir which was apparently invaded frequently by Corixids but never permanently colonized by any species. Walton (1943, pp. 255 and 262) records both *Corixa germari* and *Glaenocorisa propinqua* from deep water, and Prof. G. E. Hutchinson, in a letter, tells of a locality near Cambridge where *G. propinqua* was most easily caught through the ice. It is, therefore, noteworthy that the collection in Great Rundale Tarn was made in the middle from an inflatable boat after no Corixids had been found round the edge. Unfortunately a strong wind prevented a large catch being made. Hutchinson, who collected frequently from the bank of Great Rundale Tarn, records (*in litt.*) great numbers of *C. carinata*, but only one *Corixa germari* and no *Glaenocorisa propinqua*. Both evidently inhabit deeper water than the usual peat pool species *Corixa scotti*, *C. castanea*, *C. wollastoni* and *C. nigrolineata*, and accordingly are generally absent from small pools. Their apparent scarcity may be due in some measure to their occurring in water beyond the reach of a pond net wielded from the bank.

In subgroup IV *e* *C. wollastoni* and *C. nigrolineata* are almost the only species. Macan (1938, p. 17) records them as the only two occurring in significant numbers in the Lake District in high peat pools, the lowest of which was 1300 ft. above sea-level. Brown (1943, p. 224; 1945, p. 495; 1948, p. 193) confirms that *C. wollastoni* is almost confined to high altitudes. Popham (1949, p. 7) recorded 111 specimens in his SL 35 which is but 625 ft. above sea-level, but this catch is the product of a very long collecting effort (see his footnote to Table 2, p. 21). Apart from two, Brackenber Tarn in IV *d* and Moine Mohr 4, a peat cutting beside the sea, all the localities of the present series were at high altitudes. A height is given in Table 7 where an accurate one was recorded at the time or has been ascertainable later; localities without figures were all above 1000 ft. (300 m.), many of them far above. Why *C. wollastoni* should occur in the two low places named remains inexplicable. The pool on Dufton Fell, the only one in which *C. carinata* was taken, was large compared with the general run of such places. Brown (1945, p. 495) in a detailed study of *C. carinata* and *C. wollastoni* writes: '*carinata* tends to predominate in larger deeper pools with much open water'. Macan's (1938, p. 17) observations agree. Most, though not all of the pools in which *C. nigrolineata* predominated were shallower than those in which *C. wollastoni* was the commonest species. There is nothing to add to Macan's (1938, p. 17) discussion of the relationships of these two.

Group V. C. nigrolineata, C. punctata, C. lateralis

The break between groups IV and V has been based on the nature of the water bodies and cuts through the records of *C. nigrolineata*. A glance shows that the difference between groups IV and V is striking; apart from the connecting *C. nigrolineata*, the species of each hardly occur at all in the other. Clearly the grouping coincides with some marked ecological difference. This difference is that, whereas all the places in group IV are unproductive and of an oligotrophic or dystrophic type, those of group V, except possibly one or two in subgroup *a*, are rich or eutrophic. Not all lie in good agricultural land, but those that do not are enriched by occasional or frequent fouling by cattle or horses.

The species characterizing group V, together with *C. limitata*, were all common in dewponds, the calcareous localities studied by Macan & Macfadyen (1941). All the places are small; one is about an acre in extent but most are much less. Some have a flow through, some have not. They are arranged to give a sequence from those with *C. nigrolineata* only, through those with a varied fauna, to those with *C. lateralis* only. It is convenient to begin with these last ones (V*c*), because the habitat of *C. lateralis* is so clearly defined. The first six include a series of sewage-works ponds and five others of various types, each of which was so polluted with dung that the water was green and opaque. The last two places were beside the sea and presumably saline though no tests were made. Polluted and saline localities appear to have something in common. For example, the writer (see Classey 1944) found a typical salt-marsh mosquito, *Aedes caspius*, in fields flooded by the River Blackwater which was polluted by the overloaded W.D. sewage works at Aldershot. Possibly the common factor is high salinity. There were 47 mg./l. of chloride in the River Blackwater which is a higher concentration than is usual in waters not near the sea; water from the actual breeding-place was not analysed.

Taking V*a* next, it is less easy to define the habitat of *C. nigrolineata*. Five out of the ten small ponds were noted as being particularly shallow, though how permanent they were could not be ascertained. Walton (1943, p. 251) writes that it is 'an abundant species in small ponds in pastures and other small temporary habitats associated with farming'. Not all the haunts of this species, however, are small and shallow, and it is impossible to draw a general conclusion. Macan & Macfadyen (1941, p. 182), struck with the contrast between the calcareous dewponds they were studying and high peat pools, suggest that biological races of *C. nigrolineata* may inhabit the two sorts of place, but the postulate is no longer necessary as the present series includes all stages between the two extremes.

There remains subgroup *b*, in the six localities of which there are always at least five species and always *C. punctata*. With so few places and so varied a fauna, it would be rash to go far in drawing conclusions. Moreover, the three species characteristic of group V are some of the readiest fliers (Brown 1951, Popham 1951) and this proclivity is likely to upset the theories of ecologists analysing single collections. Nevertheless, it is proposed to base on the present data and experience elsewhere some speculations which should serve a useful purpose as an Aunt Sally if no other, and to proceed from them to a summary of all the conclusions drawn about groups II, IV, and V.

It has been shown that the ponds of group V, except for some in subgroup *a*, are eutrophic and that this separates them sharply from the places in group IV. They are, further, all quite small and this appears to be another important feature, probably the main difference between groups I and III and group V. Thus, the conditions that are about to be postulated as optimal for *C. punctata* are similar to those that have been described as optimal for *C. praeusta*; the difference is that whereas *C. punctata* is a species typical of ponds, *C. praeusta* occurs more often and more abundantly in larger bodies of water. In a small pond that has a fair amount of vegetable detritus in it and a good supply of inorganic substances to cause the organic matter to decay, or is slightly polluted by animals, several species, with *C. punctata* among the most important, might be expected. An increase in the amount of animal pollution would lead to a great abundance of *C. lateralis*. If the amount of inorganic matter is not great and the vegetable remains tend to accumulate in an undecomposed state, *C. distincta* would be the common species. It is thought that the two New Forest ponds in V*b*, which are on a base-deficient soil but somewhat polluted by ponies, and in which *C. distincta* is the most abundant species, illustrate this trend. Its culmination is the peaty or dystrophic pond containing only *C. scotti* and *C. castanea*. If the pond becomes overgrown with emergent vegetation or partly filled each autumn with leaves from nearby trees, the result will be a sparse fauna consisting mainly or entirely of *C. sahlbergi*. *C. linnei* might precede it but this may be another species found more often in larger bodies of water. As the pond decreases in depth, owing to the accumulation of plant remains, *C. nigrolineata* may be expected to become predominant. There is nothing to add to what Macan & Macfadyen (1941, p. 181) have to say about the factors that favour *C. limitata* at the expense of other species.

Nothing so far has been said about the new pond, one in which there has not been time for organic matter to accumulate on the bottom. Brown (1951) has shown that it will first be colonized by ready fliers, but what will the permanent population be? *C. venusta* was the conclusion drawn earlier, if the pond is in rock and floored with the debris of quarrying, but, if the bottom be of sand or clay, neither the present collection nor any other can provide an answer.

THE RECORDS OF OTHER WORKERS

As already explained, it was not possible to analyse these records, the sources of which are shown in Table 2, by the method just used, but their number was such that it seemed worth trying a mathematical approach, to see how well conclusions reached indirectly tallied with those derived from direct observation. A rigid mathematical technique may mislead if applied quite objectively as some authors, seeking to avoid the faintest suspicion of subjective bias, maintain that it should be, and two possible sources of error must be mentioned in connexion with the data about to be discussed. It is assumed that there is a gradient of certain factors which influence Corixidae and that different species are found along different stretches of the gradient. For example, *C. lacustris*, *C. distincta*, *C. scotti* and *C. castanea* are four species that span the gradient of the proportion of organic matter in the soil, when organic matter is accumulating and not decomposing much. It is to be expected, therefore, that *C. lacustris* would show a high degree of association with *C. distincta* and a progressively smaller one with

the other two species. If, however, the area in which conditions are right for one species is very extensive relative to the others, that species is likely to be so abundant that it intrudes into all the habitats. For example, in Windermere most of the bottom suitable for Corixids is sandy with a low percentage of organic matter, and therefore suitable for *C. lacustris*. This species, accordingly, is found in almost every collection. In tarns,

Table 2. *Sources of data*

	No. of localities listed	No. of localities used in the present analysis
Pearce & Walton (1939)	141	91
Brown (1943)	102	51
Walton (1943)	44	38
Brown (1948)	227	100
Popham (1949)	70	54
Popham (1950)	27	18
Slack (MS. records)—Derbyshire	—	29
Slack (MS. records)—Scotland	—	19
	Total	400

on the other hand, most of the bottom is generally peaty with a high percentage of organic matter, and *C. scotti* is the species that is found with all the other members of the succession. Macan & Worthington (1951, pp. 135, 136) illustrate this with two histograms. The reply is that this source of error operates only when sampling has not been sufficient, but it is a possible one that the practical field worker must bear carefully in mind nonetheless.

The second source of error arises where the gradient extends over a series of small places. There may be little overlapping of species, because, on either side of a given point, conditions will be more suitable for one species or the other, and the one that is favoured, however slightly, drives the other out completely. For example it seems unlikely that the Lake District peat pools studied by Macan (1938) were not all of the same type apart from the altitude at which they lay, yet hardly any contained members from both of two pairs of species, *C. wollastoni* and *C. nigrolineata* which occurred at higher levels, or *C. scotti* and *C. castanea* which occurred lower down. Presumably the temperature requirements of these species are different, but it seems unlikely that otherwise they are not ecologically close. This relationship would not be detected by a purely mathematical analysis.

Several workers have described ways of calculating the degree of association between species. Russell & Rao (1940), working on larvae of *Anopheles*, expressed the relationship of one species to another by calculating the number of places in which both occurred as a percentage of the places in which the species considered occurred. Mozley (1936) ascertained the relationship between two species of aquatic snails by evaluating the expression

$$\frac{\text{total ponds} \times \text{ponds with both species}}{\text{ponds with species } a \times \text{ponds with species } b}.$$

The author devised a method of calculating the association of Corixidae using not only the number of places in which two species occurred together but also their relative numbers in those places, and Brown (1945) found it of sufficient interest to publish.

One disadvantage of all these methods is that they give no indication of the significance of any result.

Agrell (1945*a*), interested in soil animals, collected samples of earth that he characterized rather exactly, for example: soil from alpine meadows, raw humus from pine wood, moss and lichen from alpine boulder region and so on, and then by means of a long calculation arrived at the 'characteristic number' for each species. A species occurring everywhere would have a characteristic number of 0, and higher numbers indicate an increasing degree of restriction of habitat range. The method depends on an accurate classification of the types of biotope at the beginning, which is not always possible. Gisin (1947) attacks Agrell's method of analysis with some vigour, and illustrates his own with Agrell's data. It is in principle the same as that used in the first part of this paper. Agrell (1945*b*) also uses the tabular method of Kulczynski, which is followed in principle in Tables 4–6 here except that they show relationships between two species as coefficients of association instead of as the number of stations where both occur expressed as a percentage of all the stations with either.

The present analysis, after advice from the Bureau of Animal Population had been obtained through the good offices of A. Macfadyen, was carried out according to the method of Cole (1949). Cole discusses what he calls the coefficient of correlation, which involves total numbers of two species caught as well as number of times they occur together, but discards it on the grounds that one or two samples in which both species, or conversely only one species, occur in great abundance weight the result unduly. His calculations are based wholly on number of times two species are found together. First he calculates χ^2 in the usual way, associating the less with the more abundant species, and discovers whether the association between the two is not significant, or positively or negatively significant or highly significant. Then he obtains a figure for the coefficient of association, which he calls C_7, by means of the following formula, in which the letters have the same meaning as in the χ^2 table:

$$C_7 = \frac{ad - bc}{(a+b)(b+d)}.$$

The standard error of this is

$$\sqrt{\frac{(a+c)(c+d)}{(a+b+c+d)(a+b)(a+c)}}.$$

The information from the sources indicated in Table 2 was extracted, sifted, stations where only a few specimens were taken being rejected, and then set out in Table 3, in which the figures show in how many places each species was found with every other. The figure at the point where horizontal and vertical columns of a species meet indicates how often that species occurred alone. The coefficient of association between the species Cole's C_7 was then calculated, and the results are presented in Tables 4–6.

The amount of light shed on the ecological relationships of Corixidae is not great and scarcely seems commensurate with the labour involved in extracting the original details from their sources and making the calculations. The chief reason is the unexpectedly large number of positive associations found. When objective analysis produces a less well-defined picture than a subjective technique, the utmost caution must be observed in an attempt to explain away the discrepancy, but it does seem fair to

Table 3. *The number of times species were found together*

	punctata	*lacustris*	*sahlbergi*	*nigrolineata*	*distincta*	*lateralis*	*falleni*	*linnei*	*praeusta*	*scotti*	*castanea*	*fossarum*	*limitata*	*venusta*	*germari*	*concinna*	*moesta*	*panzeri*	*bonsdorffi*	*stagnalis*	*wollastoni*	*coleoptrata*	*semistriata*	*poweri*	*carinata*	*dentipes*	*affinis*	*propinqua*	*selecta*	*scholtzi*	Total occurrences
Corixa punctata (Illig.)	9	55	80	64	47	62	36	48	43	17	16	25	29	10	13	18	15	15	9	10	3	9	13	2	3	10	6	2	1	1	158
C. lacustris Macan	55	7	53	31	48	32	57	41	42	19	8	22	15	9	11	13	10	14	9	6	4	10	7	9	2	4	0	3	0	4	132
C. sahlbergi (Fieb.)	80	53	8	51	36	42	27	39	32	13	10	17	18	7	8	10	15	8	4	7	4	4	10	4	1	3	2	1	0	1	125
C. nigrolineata (Fieb.)	64	31	51	10	28	52	22	23	25	19	19	17	24	14	11	9	13	7	3	5	9	5	12	2	4	1	2	3	1	0	122
C. distincta (Fieb.)	47	48	36	28	2	29	29	30	39	28	13	20	18	7	16	16	8	15	15	5	7	7	9	0	2	9	3	4	1	1	91
C. lateralis (Leach)	62	32	42	52	29	1	19	21	23	7	6	17	25	3	6	16	13	8	5	8	2	2	6	0	1	0	6	0	2	2	89
C. falleni (Fieb.)	36	57	27	22	29	19	2	20	17	14	4	15	13	9	12	13	2	13	4	2	3	10	4	7	4	3	1	2	1	2	86
C. linnei (Fieb.)	48	41	39	23	30	21	20	3	29	13	12	20	9	5	5	9	9	9	7	7	2	6	8	1	2	3	2	3	1	1	79
C. praeusta (Fieb.)	43	42	32	25	39	23	17	29	2	17	10	17	17	5	10	12	6	11	12	2	3	5	7	2	3	3	1	3	1	0	73
C. scotti ((Fieb.) D. & S.)	17	19	13	19	28	7	14	13	17	1	28	2	5	15	10	4	1	5	11	4	6	1	10	2	4	5	1	4	2	0	63
C. castanea (Thoms.)	16	8	10	19	13	6	4	12	10	28	10	1	2	7	5	4	0	2	7	2	4	0	8	0	2	3	1	1	1	0	51
C. fossarum (Leach)	25	22	17	17	20	17	15	20	17	2	1	3	10	1	3	5	5	3	3	6	0	6	6	1	0	1	3	1	0	0	45
C. limitata (Fieb.)	29	15	18	24	18	25	13	9	17	5	2	10	0	3	4	7	6	7	2	3	0	1	3	0	1	2	1	0	1	0	39
C. venusta (D. & S.)	10	9	7	14	7	3	9	5	5	15	7	1	3	3	4	1	0	3	3	0	5	0	4	4	3	0	0	2	1	1	37
C. germari (Fieb.)	13	11	8	11	16	6	12	5	10	10	5	3	4	4	0	5	1	7	6	1	7	0	4	1	6	3	2	6	1	0	28
C. concinna (Fieb.)	18	13	10	9	16	16	13	9	12	4	4	5	7	1	5	0	3	8	1	1	0	2	1	0	1	0	0	1	1	0	25
C. moesta (Fieb.)	15	10	15	13	8	13	2	9	6	1	0	5	6	0	1	3	4	6	0	2	0	2	2	0	0	0	0	0	0	0	25
C. panzeri (Fieb.)	15	14	8	7	15	8	13	9	11	5	2	3	7	3	7	8	6	0	3	1	0	5	2	0	1	2	0	1	1	0	22
Cymatia bonsdorffi (C. Sahlb.)	9	9	4	3	15	5	4	7	12	11	7	3	2	3	6	1	0	3	0	1	2	4	3	0	2	3	1	3	0	0	22
Corixa stagnalis (Leach)	10	6	7	5	5	8	2	7	2	4	2	6	3	0	1	1	2	1	1	6	0	0	4	0	0	2	4	0	2	0	21
C. wollastoni (D. & S.)	3	4	4	9	7	2	3	2	3	6	4	0	0	5	7	0	0	0	2	0	1	0	1	0	5	1	1	4	0	0	21
Cymatia coleoptrata (Fab.)	9	10	4	5	7	2	10	6	5	1	0	6	1	0	0	2	2	5	4	0	0	1	0	1	0	1	0	0	0	1	20
Corixa semistriata (Fieb.)	13	7	10	12	9	6	4	8	7	10	8	6	3	4	4	1	2	2	3	4	1	0	0	0	2	0	2	0	1	0	19
Micronecta poweri (D. & S.)	2	9	4	2	0	0	7	1	2	2	0	1	0	4	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	16
Corixa carinata (C. Sahlb.)	3	2	1	4	2	1	4	2	3	4	2	0	1	3	6	1	0	1	2	0	5	0	2	0	4	2	0	2	1	0	14
C. dentipes (Thoms.)	10	4	3	1	9	0	3	3	3	5	3	1	2	0	3	0	0	2	3	2	1	1	0	0	2	0	0	0	0	0	12
C. affinis Leach	6	0	2	2	3	6	1	2	1	1	1	3	1	0	2	0	0	0	1	4	1	0	2	0	0	0	1	0	1	0	9
Glaenocorisa propinqua (Fieb.)	2	3	1	3	4	0	2	3	3	4	1	1	0	2	6	1	0	1	3	0	4	0	0	0	2	0	0	0	0	0	9
Corixa selecta (Fieb.)	1	0	0	1	1	2	1	1	1	2	1	0	1	1	1	1	0	1	0	2	0	0	1	0	1	0	1	0	4	0	8
Micronecta scholtzi (Fieb.)	1	4	1	0	1	2	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	6

mention three factors that tend to produce an unduly high number of positive associations. The most important one is probably the ignoring of relative numbers and the treating of a single specimen in a big catch as of the same value as many specimens. Bound up with this is ignorance about Corixid movements; it is not known how often

Table 4. *Coefficients of association of species typical of dystrophic and oligotrophic waters*

(Figures in heavy type denote highly significant, others significant association.)

	wollastoni	*carinata*	*germari*	*propinqua*	*venusta*	*scotti*	*castanea*	*semistriata*	Total +	Total −
wollastoni	—	0·32	0·28	0·41	0·16	—	—	—	—	—
carinata	0·32	—	0·39	0·19	—	—	—	—	—	—
germari	0·28	0·39	—	0·64	—	0·24	—	0·15	—	—
propinqua	0·41	0·19	0·64	—	—	0·34	—	—	—	—
venusta	0·16	—	—	—	—	0·28	—	—	—	—
scotti	—	—	0·24	0·34	0·28	—	0·46	0·44	—	—
castanea	—	—	—	—	—	0·46	—	0·34	—	—
semistriata	—	—	0·15	—	—	0·44	0·34	—	—	—
Lake and river group										
bonsdorffi	—	—	0·23	0·29	—	0·41	—	0·11	4	0
distincta	—	—	0·43	—	—	0·23	—	0·47	3	0
praeusta	—	—	0·21	—	—	—	—	0·23	2	0
panzeri	—	—	0·27	—	—	—	—	—	1	0
concinna	—	—	0·14	—	—	—	—	—	1	0
poweri	—	—	—	—	0·16	—	—	—	1	0
linnei	—	—	—	—	—	—	—	0·28	1	0
falleni	—	—	0·27	—	—	—	−0·54	—	1	1
fossarum	—	—	—	—	—	−0·72	−0·85	0·23	1	2
lacustris	—	—	—	—	—	—	−0·52	—	0	1
coleoptrata	—	—	—	—	—	—	—	—	0	0
Pond group										
dentipes	—	—	0·19	—	—	0·31	—	—	2	0
affinis	—	—	—	—	—	—	—	0·18	1	0
stagnalis	—	—	—	—	—	—	—	0·17	1	0
nigrolineata	—	—	—	—	—	—	—	0·46	1	0
punctata	−0·64	—	—	—	−0·58	−0·35	—	0·48	1	3
sahlbergi	—	−0·83	—	—	—	−0·34	−0·37	0·31	1	3
lateralis	—	—	—	—	−0·64	−0·50	−0·47	—	0	3
limitata	—	—	—	—	—	—	—	—	0	0
moesta	—	—	—	—	—	—	—	—	0	0
selecta	—	—	—	—	—	—	—	—	0	0

species drop into places that do not provide a typical habitat for them, nor how long they stay when this does happen, and there are no means of recognizing such extraneous species in a catch. That they bias association calculations based on single collections cannot be doubted, but the extent to which they may do so is unknown. Two other factors, probably of less importance, are first the likelihood that some of the catches were obtained by sweeping through the habitat of more than one species; Macan (1938, p. 15) mentions two stations which were barely 1 m. apart and had almost totally different populations, and there is no evidence that other collectors had the same interest in detailed observation of this kind. Secondly, there may have been a deliberate choice of places that seemed likely to yield a varied fauna; Walton (1943,

p. 254) states that he did not study *C. sahlbergi* sufficiently because 'the type of habitat where it occurs most abundantly was so uninteresting to the writer' the places being 'characterized by paucity of their fauna and the monotony of their flora'. Primary information of the type used here is bound to be subject to all these factors.

Table 5. *Coefficients of association of lake and river species*

(Figures in heavy type denote highly significant, others significant association.)

	lacustris	*falleni*	*poweri*	*coleoptrata*	*panzeri*	*bonsdorffi*	*distincta*	*praeusta*	*fossarum*	*limnei*	*concinna*	Total +	Total −
stris	—	**0·43**	0·35	**0·42**	**0·46**	—	**0·30**	**0·37**	**0·24**	**0·28**	0·28	—	—
eni	**0·43**	—	**0·28**	**0·36**	**0·48**	—	**0·14**	—	0·15	—	**0·39**	—	—
eri	0·35	**0·28**	—	—	—	—	—	—	—	—	—	—	—
optrata	**0·42**	**0·36**	—	—	**0·21**	**0·15**	—	—	**0·21**	—	—	—	—
zeri	**0·46**	**0·48**	—	**0·21**	—	0·10	**0·59**	**0·38**	—	**0·26**	**0·44**	—	—
dorffi	—	—	—	**0·15**	0·10	—	**0·59**	**0·44**	—	—	—	—	—
incta	**0·30**	**0·14**	—	—	**0·59**	**0·59**	—	**0·40**	**0·28**	**0·19**	**0·53**	—	—
eusta	**0·37**	—	—	—	**0·38**	**0·44**	**0·40**	—	**0·22**	**0·25**	**0·36**	—	—
arum	**0·24**	0·15	—	**0·21**	—	—	**0·28**	**0·22**	—	**0·30**	—	—	—
ei	**0·28**	—	—	—	**0·26**	—	**0·19**	**0·25**	**0·30**	—	0·20	—	—
cinna	0·28	**0·39**	—	—	**0·44**	—	**0·53**	**0·36**	—	0·20	—	—	—
group													
ctata	—	—	—	—	**0·47**	—	**0·20**	**0·32**	0·27	**0·34**	**0·54**	6	0
lbergi	**0·14**	—	—	—	—	—	0·12	**0·20**	—	**0·26**	—	4	0
tata	—	—	—	—	**0·24**	—	**0·30**	**0·31**	**0·15**	—	—	4	0
ralis	—	—	—	—	—	—	**0·13**	**0·12**	—	—	**0·54**	3	0
tipes	—	—	—	—	—	**0·20**	**0·68**	—	—	—	—	2	0
sta	—	−0·72	—	—	**0·31**	—	—	—	—	0·20	—	2	1
nalis	—	—	—	—	—	—	—	—	**0·20**	—	—	1	0
olineata	−0·23	—	−0·59	—	—	−0·55	—	—	—	—	—	0	3
nis	—	—	—	—	—	—	—	—	—	—	—	0	0
cta	—	—	—	—	—	—	—	—	—	—	—	0	0
trophic-dystrophic group													
nari	—	**0·27**	—	—	**0·27**	**0·23**	**0·43**	**0·21**	—	—	0·14	6	0
istriata	—	—	—	—	—	0·11	**0·47**	0·23	**0·23**	**0·28**	—	5	0
pinqua	—	—	—	—	—	**0·29**	—	—	—	—	—	1	0
usta	—	—	0·16	—	—	—	—	—	—	—	—	1	0
ti	—	—	—	—	—	**0·41**	**0·23**	—	−0·72	—	—	2	1
anea	−0·52	−0·54	—	—	—	—	—	—	−0·85	—	—	0	3
lastoni	—	—	—	—	—	—	—	—	—	—	—	0	0
inata	—	—	—	—	—	—	—	—	—	—	—	0	0

In particular, Cole's objection to combining relative abundance and number of times together is specially strong when collections not made in a standard way are under analysis.

A preliminary glance at the results shows that the species typical of dystrophic and oligotrophic conditions, those of group IV of the previous analysis, form a rather distinctly separate group, and accordingly they are taken first, the associations being shown in Table 4. The first four species, *C. wollastoni*, *C. carinata*, *C. germari* and *Glaenocorisa propinqua* are all closely associated with one another, and the last three *Corixa scotti*, *C. castanea*, and *C. semistriata* for a similar subgroup. In each of these subgroups there is one species that has wide associations with species of different

habitats; *C. germari* of the first subgroup is associated with lake species even with the calciphile *C. falleni* which is surprising, though in keeping with what the earlier analysis revealed; *C. semistriata* of the second subgroup is associated with both pond and lake species, which suggests that the earlier definition of its habitat attempted a sharper

Table 6. *Coefficients of association of species characteristic of productive ponds*

(Figures in heavy type denote highly significant, others significant association.)

	lateralis	*limitata*	*nigrolineata*	*punctata*	*sahlbergi*	*moesta*	*dentipes*	*affinis*	*stagnalis*	*selecta*	Total +
lateralis	—	**0·54**	**0·40**	**0·51**	**0·22**	**0·38**	—	**0·57**	—	—	—
limitata	**0·54**	—	**0·45**	**0·60**	0·22	**0·16**	—	—	—	—	—
nigrolineata	**0·40**	**0·45**	—	**0·20**	0·15	0·31	—	—	—	—	—
punctata	**0·51**	**0·60**	**0·20**	—	**0·41**	0·34	**0·72**	0·45	—	—	—
sahlbergi	**0·22**	0·22	0·15	**0·41**	—	**0·42**	—	—	—	—	—
moesta	**0·38**	**0·16**	0·31	0·34	**0·42**	—	—	—	—	—	—
dentipes	—	—	—	**0·72**	—	—	—	—	—	—	—
affinis	**0·57**	—	—	0·45	—	—	—	—	**0·41**	—	—
stagnalis	—	—	—	—	—	—	—	**0·41**	—	**0·21**	—
selecta	—	—	—	—	—	—	—	—	**0·21**	—	—
Lake and river group											
distincta	**0·13**	**0·30**	—	**0·20**	0·12	—	**0·68**	—	—	—	5
praeusta	**0·12**	**0·31**	—	**0·32**	**0·20**	—	—	—	—	—	4
linnei	—	—	—	**0·34**	**0·26**	0·20	—	—	—	—	3
fossarum	—	**0·15**	—	0·27	—	—	—	—	**0·20**	—	3
panzeri	—	**0·24**	—	**0·47**	—	**0·31**	—	—	—	—	3
concinna	**0·54**	—	—	**0·54**	—	—	—	—	—	—	2
bonsdorffi	—	—	−0·55	—	—	—	**0·20**	—	—	—	1
lacustris	—	—	−0·23	—	**0·14**	—	—	—	—	—	1
falleni	—	—	—	—	—	−0·72	—	—	—	—	0
poweri	—	—	−0·59	—	—	—	—	—	—	—	0
coleoptrata	—	—	—	—	—	—	—	—	—	—	0
Oligotrophic-dystrophic group											
semistriata	—	—	**0·46**	**0·48**	0·31	—	—	**0·18**	**0·17**	—	5
germari	—	—	—	—	—	—	**0·19**	—	—	—	1
wollastoni	—	—	—	−0·64	—	—	—	—	—	—	0
scotti	−0·50	—	—	−0·35	−0·34	—	**0·31**	—	—	—	1
venusta	−0·64	—	—	−0·58	—	—	—	—	—	—	0
castanea	−0·47	—	—	—	−0·37	—	—	—	—	—	0
carinata	—	—	—	—	−0·83	—	—	—	—	—	0
propinqua	—	—	—	—	—	—	—	—	—	—	0

restriction than is actually the case. The rest show few outside associations except for some negative ones. Unexpected is the negative association between *C. sahlbergi* and *C. castanea* because the habitats of the two merge one into the other. Macan (1938, pp. 13 and 14) took *C. fossarum* and *C. scotti* fairly often in the same tarn, but an examination of his table 6 shows that the only 5 stations out of 37 where neither *C. scotti* nor *C. castanea* was numerous were those where *C. fossarum* predominated; the negative association found here agrees with the observations of Brown (1948, p. 191).

The names of those which, for want of a better name, may be called the group IV species are set out along both axes of Table 4, the rest only vertically. Of the latter, *Cymatia bonsdorffi* and *Corixa distincta*, and to a lesser extent, *C. praeusta* and *C. dentipes*,

tend to be associated with the group IV species, whereas *C. punctata*, *C. sahlbergi*, and *C. lateralis* show several negative associations.

The species not in group IV are less easy to arrange, though it is possible to distinguish on the one hand lake and river species, groups I and III of the preceding analysis, and on the other pond species, the previous groups II and V, and their associations are shown in separate tables.

The lake group is set out in Table 5. The first four species are associated with each other but have few associations with species in either of the other groups. *C. bonsdorffi* is closely associated with the group IV species and might indeed have been included among them. The remaining species all have wide outside associations mainly with species in the pond group. Outside species that have close associations with the lake group are *C. punctata*, *C. germari* and *C. semistriata*. *C. panzeri* is one of the few rare species in Britain; Sutton (1947) found enough in Emergency Water Supply tanks in London to work on its life history, Brown (1943) found 38 of which 36 were in one pool, Walton (1943) took 36 specimens of which 15 were in one pond, and the other authors including the writer record the species only in one's and two's. It emerges clearly from the present analysis as a member of the lake group. It is satisfactory to find that the association of *C. concinna* with *C. lacustris* and *C. falleni* on one hand, and with *C. lateralis* on the other, is as clear in this analysis as it was in the previous one. The mathematical technique is probably particularly valuable in revealing the relationships of the rare species.

Table 6 shows the associations of the pond species. Each of the first six is associated with every other, the first four (*C. lateralis*, *C. limitata*, *C. nigrolineata* and *C. punctata*), that is the species characteristic of group V above, all being closely associated, the last two (*C. sahlbergi* and *C. moesta*) less so. *C. nigrolineata* has three negative associations with species of the lake-river group, but the other species show some or considerable association with it. *C. semistriata*, evidently a species of catholic taste, connects the group IV species and the pond species, which otherwise are little associated, the three negative associations of *C. lateralis* and *C. punctata* standing out conspicuously. *C. dentipes*, one of the less common corixids, has been included in this group because its association with *C. punctata*, to which it is closely related morphologically, is so high. Its other associations are with two group IV species and with two lake species both associated with that group.

C. selecta is the only species in the whole list with but one association, which is not surprising because it is a saltmarsh species. So also is its associate, *C. stagnalis*. The latter has wider connexions, and is associated with the rare *C. affinis*, and with *C. fossarum* and *C. semistriata*, both of which were noted by Lindberg (1937) in Finland as being more tolerant of salinity than other species except *C. striata*.

With so many species associated with so many others, it is evident that any diagrammatic representation would be much too involved to throw any light on relationships. Moreover, it is as well to bear in mind the fundamental difficulties inherent in any attempt to set out within the two dimensions of a sheet of paper interrelationships that depend on many varying factors. None the less, it is of interest to select the commonest species and see if any graphical representation of their relationships is possible. Eleven species were taken more than 50 times, and this number is likely to

be as high as is compatible with a reasonably clear diagram. As a further simplification, it is convenient to consider for a start only those associations which were highly significant by the χ^2 test. Each of these species was associated with others thus:

castanea	with 1 other species
scotti, falleni, nigrolineata	with 2 other species
lacustris, sahlbergi, linnei, lateralis	with 5 other species
punctata, praeusta	with 6 other species
distincta	with 7 other species

In any diagrammatic scheme the species associated with few others must obviously be at the margin, those with many in the middle. Of the four species with two associations or fewer, *C. castanea* is closely associated with *C. scotti* and must obviously come near to it, and negatively associated both with *C. falleni* and *C. lacustris*, which

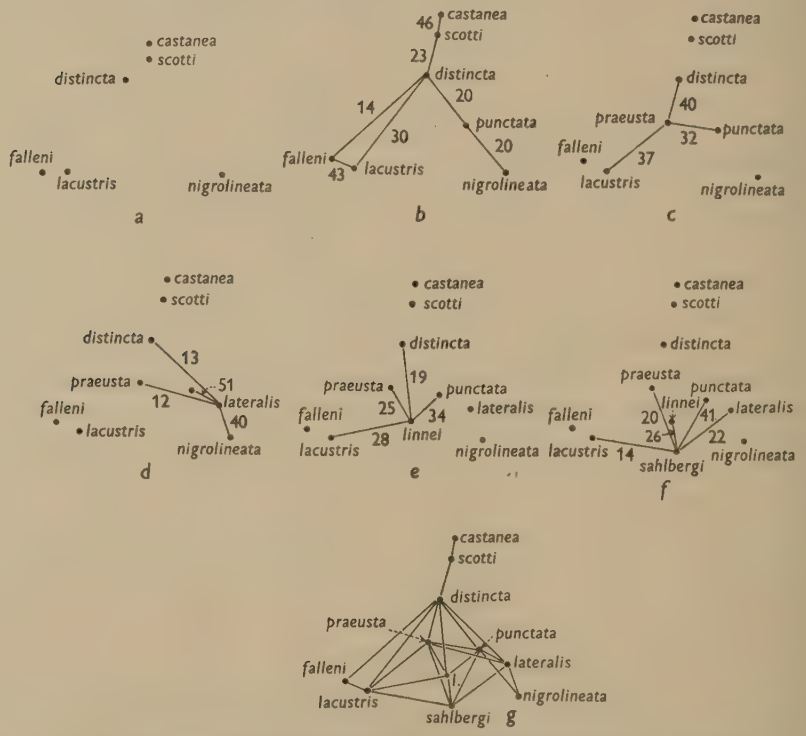


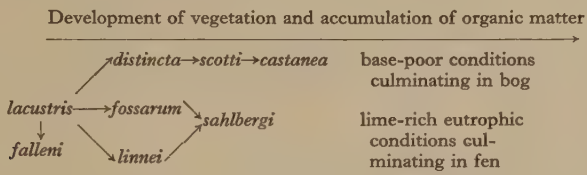
Fig. 1. A diagrammatic representation of the ecological relationships of Corixidae.

form another pair close together. It is not associated positively or negatively with *C. nigrolineata* but it has a negative association with *C. lateralis* and *C. scotti* has a negative association with *C. punctata*, so there is negative association between this pair and the close associates of *C. nigrolineata*. *C. nigrolineata* is negatively associated with *C. lacustris*. Between *C. scotti* and *C. castanea* together, *C. nigrolineata*, and the pair *C. lacustris* and *C. falleni* there is, therefore, least ecological affinity and these species may be placed at the corners of a triangle. *C. scotti* and *C. lacustris* must be

a little inside their partners because they have more associations. *C. distincta* is the only one of the remaining species associated with *C. scotti*, and it must obviously go near that species and toward *C. lacustris* and *C. falleni*, because it is associated with them but not with *C. nigrolineata*. In this way Fig. 1*a* is arrived at.

C. punctata, another species with many associations, is associated with *C. distincta* and *C. nigrolineata*, the C_7 values being the same, and is not associated with *C. lacustris* or *C. falleni*. Clearly it must go towards the right-hand side of the figure, equidistant from *C. distincta* and *C. nigrolineata*. At this point associated species may be joined by lines, a long line for a low coefficient of association and vice versa, a procedure which pulls *C. falleni* up towards *C. distincta* and lengthens the distance between that species and *C. scotti*. This gives Fig. 1*b*. The removal of these lines, and the introduction of *C. praeusta* with lines connecting it to each species with which it is associated gives Fig. 1*c*. *C. lateralis* slips easily into the figure (Fig. 1*d*), and so does *C. linnei* (Fig. 1*e*). The last species, *C. sahlbergi*, though rather far from its closest associate, *C. punctata*, fits in well otherwise (Fig. 1*f*), and the complete figure (Fig. 1*g*) does seem on the whole to be a fair representation of the relationships of these eleven species.

Macan (in press) summarizes the data from lakes of various types and from dystrophic tarns in the following scheme:



When the two are compared it is evident that the main difference is the absence from Macan's scheme of *C. punctata*, *C. nigrolineata* and *C. lateralis*, which is to be expected since they are species of eutrophic ponds, a type of place that he was not considering. *C. praeusta* is also absent, not because it was not recorded but because Macan did not know where to put it, a difficulty of which perhaps at least a part explanation is that it is, as suggested earlier, a species neither of the undoubted lake nor of the typical pond but of something intermediate in size between the two.

Macan's scheme includes *C. fossarum* which the present one does not because it was not recorded from 50 places. It has a highly significant association with *C. lacustris*, *C. distincta*, *C. praeusta* and *C. linnei*, and a significant association with *C. falleni* and *C. punctata*, and therefore occupies a left-centre position on Fig. 1*g*. If it is inserted and the pond species removed, there is a reasonably good agreement between this diagram and Macan's earlier scheme; the main points of difference are that the present figures show no association between *C. fossarum* and *C. sahlbergi* and a positive one between *C. falleni* and *C. distincta*.

A general review of the mathematical analysis that has just been completed shows that it confirms, in general, conclusions reached earlier in this article and elsewhere, though the picture that emerges is more blurred than previous ones.

ACKNOWLEDGEMENTS

The laborious task of bringing together the information of the other authors, who describe their collecting places on one page and list the species found on another, and then calculating χ^2 and C_7 has been carried out by Mrs Jean Mackereth. I thank also Miss Charlotte Kipling and Mr E. D. Le Cren for help with statistical matters.

SUMMARY

1. One hundred and seventeen miscellaneous collections of corixids made by the author are analysed, the principle being to arrange the collecting places into groups according to the predominant species and then look for features common to each group. Frequent comparisons with the findings of other workers are made. The following arrangement emerges:

Group I. *Corixa lacustris*, *C. falleni* and sometimes *C. concinna*; rivers, ditches, lakes and one pond. *C. lacustris* occurs at almost every station; *C. falleni* has a more restricted habitat being absent from the more exposed stations and from lime-deficient waters; *C. concinna*, a rare species, is possibly associated with a salinity higher than is usual in inland waters. *C. distincta* and *C. fossarum* replace *C. lacustris* in sheltered places where organic matter accumulates.

Group II. *C. sahlbergi*; stagnant usually small places with much decomposing vegetable matter. Other species are few.

Group III. *C. praeusta*; rivers, large ponds, and small lakes that are highly productive, somewhat polluted or enriched by dead leaves. All the group I species occur frequently. *C. praeusta*, known to be a ready flier, is predominant in two recently filled ponds.

Group IV. *C. scotti*, *C. castanea*, *C. semistriata*, *C. venusta*, *C. germari*, *C. wollastoni*, *C. nigrolineata*; mountain, moorland, heath, bog, or in one instance fen pools, ponds and streams. *C. scotti* and *C. castanea* are the two species most typical of lime-deficient conditions. At high altitudes they give place to *C. wollastoni* and *C. nigrolineata*. *C. venusta* is sometimes found in ponds where it is difficult to see why *C. scotti* is not the main species and it occurs in small numbers in high pools. It is, however, found most often in running water, and there are several records of it in quarry pools in which the bottom is covered with the debris of quarrying. *C. semistriata* sometimes occurs with *C. scotti* and *C. castanea* but more commonly in small pools in fen peat. *C. germari* and *Glaenocorisa propinqua* seem to be typical of large shallow places with a uniform depth and inhabit the deeper water.

Group V. *Corixa nigrolineata*, *C. punctata*, *C. lateralis*; productive ponds. In a typical pond with plenty of vegetation there will be at least four or five species with *C. punctata* among the commonest. *C. lateralis* is favoured by intense animal fouling and is found also in ponds near the sea. The habitat of *C. nigrolineata* is less easy to define; many of the places are small and shallow. Apart from two specimens in group III, *C. limitata* was found only in group V.

2. Methods of calculating degree of association between species are discussed.

3. Information is extracted from various published papers and some MS. records, and the coefficients of association between the species of corixid from 400 places are calculated by Cole's method.

4. An unexpectedly high number of positive associations are found and reasons for this are discussed.

5. The species can be arranged, according to their associates, in three groups which coincide well with those of the previous analysis. These groups are: pools and ponds on base-poor soil (group IV), productive ponds (groups II and V), and lakes and rivers (groups I and III). The first, if two species be excluded, has few outside associations, the second and third have many common associations.

6. A diagrammatic representation of the relationships of the eleven most common species, based on the coefficients of association, is found to agree fairly well with a figure based on subjective analysis.

7. On the whole the results of the mathematical analysis tally well with subjective conclusions and are particularly useful in revealing relationships of rare species.

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Table 7. *The author's miscellaneous collections of Corixidae*

The letters following place-names indicate vice-counties.

Group				*lacustris*	*falleni*	*concinna*	*sahlbergi*	*linnei*	*praeusta*	*fossarum*	*distincta*	*bonsdorffi*	*venusta*	*semistriata*	*scotti*	*castanea*	*germari*	*wollastoni*	*nigrolineata*	*punctata*	*limitata*	*lateralis*
I*a*	R. Winster	WL	River with stony bottom	11	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
	R. Misbourne	BX	River with gravel bottom	68	—	—	6	1	2	—	—	—	—	—	—	—	—	—	—	2	—	—
I*b*	R. Brathay	WL	River	27	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Blelham Beck	WL	River	27	—	—	—	—	—	5	1	—	—	—	—	—	—	—	—	—	—	—
	Congo	WL	River	30	2	—	—	—	—	11	1	—	—	—	—	—	—	—	—	—	—	—
	Cunsey Beck	WL	River	22	4	—	—	—	1	5	1	—	—	—	—	—	—	—	—	—	—	—
I*c*	R. Wey	SR	River	16	5	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
	Swaffham Bulbeck	CB	Fen ditch	18	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—
	Bottisham Lode	CB	Fen river	6	4	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
	Malldraeth Marsh	A	Sluggish river	28	6	—	—	—	9	—	—	—	—	—	—	—	—	—	—	—	—	—
	R. Wey	SR	Oxbow	10	10	—	7	—	—	—	7	—	—	—	2	—	—	—	—	7	—	—
	Helsington Moss	WL	Ditch	9	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Swaffham Bulbeck Lode	CB	Fen river	5	12	—	1	—	—	6	—	—	—	—	—	—	—	—	—	—	—	—
I*d*	Upper Bitnell Reservoir	WO	Artificial reservoir	—	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Loch Leven, st. 1	KF	Calcareous lake	9	4	—	—	—	1	—	—	—	—	—	—	—	—	6	—	—	—	—
	Loch Leven, st. 2	KF	Calcareous lake	9	—	—	—	—	1	—	1	—	—	—	—	—	1	9	—	—	—	—
	Loch Leven, st. 3	KF	Calcareous lake	74	45	1	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
	Llyn Coron, st. 1	A	Calcareous lake	7	33	1	—	—	9	—	—	—	—	—	—	—	—	—	—	—	—	1
	Llyn Coron, st. 2	A	Calcareous lake	9	7	—	—	—	6	—	—	—	—	—	—	—	—	—	—	—	—	—
	Llyn Coron, st. 3	A	Calcareous lake	1	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Llyn Coron, st. 4	A	Calcareous lake	16	—	—	1	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—
	Llyn Hendref, st. 1	A	Calcareous lake	82	295	—	—	—	25	—	3	—	—	1	—	—	—	—	—	16	—	2
	Llyn Hendref, st. 2	A	Calcareous lake	11	—	—	14	—	—	4	—	—	—	1	—	—	—	—	—	2	—	—
I*e*	Penmon Priory	A	Pond	14	27	21	1	—	33	—	—	—	—	—	—	—	9	—	—	34	—	—
	Loch Gelly	KF	Calcareous lake	—	—	31	—	—	—	—	—	—	—	—	—	—	7	—	—	—	—	—
	Total specimens			509	485	54	30	1	90	33	18	—	—	2	2	—	17	15	—	63	—	4
	Number of stations (total 25)			23	17	4	6	1	10	6	9	—	—	2	1	—	3	2	—	6	—	3

Table 7 (*cont.*)

Group				*lacustris*	*falleni*	*concinna*	*sahlbergi*	*linnei*	*praeusta*	*fossarum*	*distincta*	*bonsdorffi*	*venusta*	*semistriata*	*scotti*	*castanea*	*germari*	*wollastoni*	*nigrolineata*	*punctata*	*limitata*	*lateralis*
II	Swaffham Bulbeck 3	CB	Fen pool	—	—	—	4	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—
	Easthampstead Millpond	BK	Pond with dead leaves	—	—	—	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Rusland Moss	WL	Peat pools	—	—	—	68	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—
	Foulshaw Moss	WL	Peat cutting	—	—	—	25	—	1	—	—	—	1	5	—	—	—	—	6	—	—	—
	Malham Carr	MY	Fen pool	—	—	—	20	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—
	Total specimens			—	—	—	128	5	2	—	—	—	1	5	—	—	—	2	8	—	—	—
	Number of stations (total 5)			—	—	—	5	1	2	—	—	—	1	1	—	—	—	1	2	—	—	—
III	R. Blackwater, st. 1	NH/SR	Polluted river	10	6	—	10	2	7	1	3	—	—	—	—	—	—	—	1	10	—	2
	R. Blackwater, st. 2	NH/SR	Polluted river	17	7	—	—	1	32	1	3	—	—	—	—	—	—	—	—	4	1	—
	R. Cree	KB	Slow river	1	—	—	—	—	8	12	12	1	—	—	—	—	—	—	—	—	—	—
	Butterby Marsh	DM	Detached loop of river	—	—	—	—	1	24	8	17	—	—	—	—	—	—	—	—	—	—	—
	Innom.	WW	Large pond	—	1	—	—	—	24	6	9	—	—	1	—	—	—	—	—	6	—	1
	Helton Lake	WL	3 stations in reeds—west	44	21	—	—	—	52	15	13	17	—	—	—	—	—	—	—	—	—	—
	Helton Lake	WL	11 stations near middle	118	90	—	—	—	18	18	19	23	14	—	—	—	—	—	—	—	—	—
	Helton Lake	WL	3 stations in reeds—east	27	10	—	1	—	5	11	5	1	—	—	—	—	—	—	—	—	—	—
	Headley's Tarn June 1939	WL	New artificial tarn	—	—	—	—	—	63	—	—	—	—	—	—	—	—	—	—	—	—	—
	Headley's Tarn April 1940	WL	New artificial tarn	1	1	4	—	—	27	1	16	1	—	—	1	—	2	—	—	—	—	—
	Headley's Tarn Nov. 1940	WL	New artificial tarn	—	5	—	—	—	2	12	22	6	—	1	3	—	1	—	—	—	—	—
	Rulbuts Tarn	WL	Tarn	—	—	—	—	—	11	—	—	—	1	—	4	2	—	—	13	—	1	—
	Droitwich	WO	Canal	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
	Basingstoke canal	SR	Canal	—	1	—	1	1	1	5	—	—	—	—	—	—	—	—	—	2	—	—
	Total specimens			219	142	4	12	5	274	90	119	49	15	2	9	2	3	—	14	22	2	3
	Number of stations (total 14)			8	9	1	3	4	13	11	10	6	2	2	4	1	2	—	2	4	2	2

IV*a*	Loch Barnluasgan	CT	Mountain lochan, alt. 1100 ft.	—	—	—	—	—	1	—	10	1	—	—	7	—	—	—	—	—	—	—
	The Flashes	SR	Heath pond, *Sphagnum*	—	—	—	—	—	—	—	—	—	—	—	1	16	—	—	—	—	—	1
	The Flashes	SR	Heath pond, sandy bottom	—	—	—	—	—	—	—	2	—	—	—	20	—	—	—	—	—	—	6
	Rannoch Moor	PN	Peat pool, alt. 950 ft.	—	—	—	—	—	1	—	1	21	5	—	12	1	—	—	—	—	—	—
	Wareham Heath	DT	Peat pool	—	—	—	—	—	—	—	—	11	—	—	—	3	—	—	—	—	—	—
	Moine Mohr 2	AM	Peat cutting near sea	—	1	—	—	1	2	—	—	—	—	14	—	—	—	—	—	—	—	—
	Tarn Haws, Silverdale	WL	Fen pools	—	—	—	1	—	—	—	—	—	—	9	—	—	—	—	—	—	—	—
	Gormer Lake	BK	Heath pond in wood	—	—	—	1	—	—	—	1	—	—	19	25	131	—	—	—	—	—	—
	Neilson Hot Blast	KB	Moorland pool	—	—	—	5	—	2	—	—	—	—	3	1	10	—	—	3	2	—	—
IV*b*	Lochan Lurg	KF	Mountain lochan, alt. 750 ft.	—	—	—	3	—	—	—	1	—	—	—	11	—	—	—	1	—	—	—
	Rhos Hirwaen	CR	Artificial moorland pond	—	—	—	9	—	—	—	—	—	—	—	—	14	—	—	—	1	—	—
	Hatchet Pond 1	SH	Heath pond	—	—	—	—	—	—	—	—	—	—	—	—	10	—	—	—	—	—	—
	Bodmin Moor	EC	Peat pool	—	—	—	—	—	—	—	—	—	—	—	3	6	—	—	—	—	—	—
	Pottery pit 2	DT	Heath pond	—	—	—	—	—	—	—	—	—	—	—	7	16	—	—	—	—	—	—
	Killin Reservoir	PM	Swamp on site of old reservoir	—	—	—	1	—	—	—	—	—	—	—	—	11	—	2	—	—	—	—
IV*c*	Kiells	CT	Small ditch	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	3	—	—	—
	Ditchend	SH	Field drains	—	—	—	—	—	—	—	—	—	13	—	—	—	—	—	7	—	—	—
	Colthouse Beck	WL	Ford across mountain beck	—	—	—	—	—	—	—	—	—	11	—	—	—	—	—	6	—	—	—
	Loch Sween	CT	Small ditch	2	—	—	—	—	—	—	—	—	10	—	—	—	—	—	—	—	—	—
	Glow Loch outflow	KF	Moorland stream	—	—	—	—	—	—	—	—	—	20	—	—	—	—	—	—	—	—	—
	Waterson Moss	WL	Drain through peat	—	—	—	1	—	3	—	2	—	9	—	—	—	—	—	1	—	—	—
	Lochan Lairig	PM	Mountain lochan	—	—	—	—	—	—	—	—	—	12	—	1	—	—	1	—	—	—	—
	Carnbrae	WC	Quarry pond	—	—	—	—	—	—	—	—	—	4	—	2	2	—	—	—	—	—	—
	Hatchet Pond 4	SH	Heath pond	—	—	—	1	—	—	—	—	—	6	—	11	13	—	—	—	—	—	—
	Kinardochy, pool 1	PM	Mountain pool	—	—	—	—	—	—	—	—	—	3	—	—	17	3	—	—	—	—	—
	L. Kinardochy inflow	PM	Mountain stream	—	—	—	—	—	1	—	2	—	10	—	9	—	9	—	—	—	—	—
	Loch Trool	KB	Mountain lochan	—	—	—	—	—	—	—	—	1	—	—	8	—	3	2	—	—	—	—
IV*d*	Moine Mohr 1	AM	Pond in peat near sea	—	—	—	—	—	15	—	1	—	—	3	—	1	27	1	3	2	—	—
	Loch Kinardochy	PM	Mountain lochan, alt. 1500 ft.	—	—	—	2	—	2	—	4	—	—	—	—	—	47	4	1	—	—	—
	Great Rundale Tarn	WL	Mountain tarn, alt. 2250 ft.	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—	—	—	—
	Brackenber Tarn, st. 1	WL	Moorland tarn, alt. 600 ft.	—	—	—	—	—	—	—	1	—	—	—	1	—	33	30	—	1	—	—
	Brackenber Tarn, st. 2	WL	Moorland tarn, alt. 600 ft.	—	—	—	—	—	—	—	—	—	—	—	1	—	6	69	—	1	—	—

Table 7 (*cont.*)

Group				*lacustris*	*falleni*	*concinna*	*sahlbergi*	*linnei*	*praeusta*	*fossarum*	*distincta*	*bonsdorffi*	*venusta*	*semistriata*	*scotti*	*castanea*	*germari*	*wollastoni*	*nigrolineata*	*punctata*	*limitata*	*lateralis*
IV*e*	Dufton Fell	WL	Peat pool, alt. 2250 ft.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	—	—	—	—
	Ringinglow Bog	WY	Moorland pool, alt. 1350 ft.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—
	Kinder Scout	DY	Mountain pool, alt. 1600 ft.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—
	Meall Sgallachd 2	PM	Mountain pool	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	—	—	—	—
	Near Loch Skeen	DF	Mountain pool, alt. 1700 ft.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	—	—	—	—
	Mickle 4	WL	Mountain pool	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	1	—	—	—
	Moine Mohr 4	AM	Peat cutting near sea	—	—	—	1	—	—	—	—	—	—	—	—	—	—	10	3	—	—	—
	Mickle 3	WL	Mountain pool	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	5	—	—	—
	Kinder Scout	DY	Mountain pool, alt. 2000 ft.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	5	—	—	—
	Cruac Lussac	CT	Mountain pool, alt. 1100 ft.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	10	—	—	—
	Mickle 2	WL	Mountain pool	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	14	—	—	—
	Meall Sgallachd 1	PM	Mountain pool, alt. 1600 ft.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	11	—	—	—
	Kinardochy pool 2	PM	Mountain pool, alt. 1500 ft.	—	—	—	2	—	—	—	—	—	—	—	—	1	—	1	12	—	—	—
	Mickle 5	WL	Small moorland pond	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	26	—	—	—
	Malham Bog	MY	Moorland pool, alt. 1250 ft.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	—	—	—
	Mickle 1	WL	Moorland pool	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	—	—	—
	Total specimens			2	1	—	27	1	28	—	25	34	106	48	120	252	132	215	133	7	—	7
	Number of stations (total 48)			1	1	—	11	1	9	—	10	4	12	5	16	15	8	21	19	5	—	2

V*a*	Cockhill Pond	PC	Small field pond	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	10	—	—	—
	Grange Farm	SH	Field pond	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	27	—	—	—
	St Ives	WC	Pool	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	—	—	—
	Haverthwaite 2	WL	Peat cutting	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	—	—	—
	Quarrington	DM	Field pond	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	—	—	—
	Frensham	SR	Pool in bed of empty pond	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	—	—	1
	Wellingore 1	LS	Field pond	—	—	—	7	—	—	—	—	—	—	—	—	—	—	—	9	—	—	1
	Wellingore 4	LS	Field pond	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	—	—	6
	Waddington	LS	Village pond	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	7	—	—
	Waddington	LS	Brick pits	1	—	—	—	5	11	—	—	—	—	—	—	—	—	—	12	3	—	—
V*b*	Swaffham Bulbeck 2	CB	Brick pit	10	1	—	1	4	1	—	—	—	—	—	—	—	—	—	—	7	—	—
	Clifton Dykes	WL	Field pond	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	4	13	3	7
	Longcross	SH	New Forest pond	—	—	—	—	—	1	—	18	1	—	—	—	—	1	—	—	3	9	—
	Janesmoor	SH	New Forest pond	1	—	4	—	—	—	—	42	—	—	—	1	—	6	—	—	1	—	4
	Horsley 1	SR	Field pond	—	—	—	—	1	2	—	—	—	—	—	—	1	—	—	—	4	10	4
	Horsley 2	SR	Field pond	—	—	—	3	—	1	—	—	—	—	—	—	—	—	—	13	7	—	14
V*c*	High Goose Farm	DM	Field pond	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	4	3	5	22
	Welwyn Sewage Wks	HT	Outfall settling ponds	12	—	12	—	—	10	—	1	—	—	—	—	—	—	—	1	1	—	111
	Seaton Sluice	SN	Field pond	2	—	1	—	—	1	—	—	—	—	—	—	—	1	—	1	—	—	34
	Wardlow Hay Cop	DY	Dewpond	—	—	—	—	—	—	—	—	—	—	—	—	—	9	—	—	4	—	31
	High Goose Farm	DM	Farmyard pond	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14
	Farne Is.	NN	Rock pools	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19
	Solway 3	CU	Pond near sea	3	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	51
	Meathop Marsh	WL	Pond near sea	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	13
	Total specimens			32	5	19	11	10	28	—	62	1	—	—	1	3	17	1	158	54	27	332
	Number of stations (total 24)			8	2	5	3	3	8	—	4	1	—	—	1	2	4	1	15	12	4	15

Other species taken were: *Cymatia coleoptrata*, Droitwich canal, 6; Basingstoke canal, 13 (III). *Corixa moesta*, R. Misbourne, 4 (I*a*); Llyn Hendref, 2 (I*d*); R. Blackwater, 2 (III); Hatchet Pond, 4 (IV*b*); Janesmoor, 1 (V*b*). *C. carinata*, Dufton Fell, 19 (IV*e*). *Glaenocorisa propinqua*, Moine Mohr 1, 1; Loch Kinardochy, 2; Great Rundale Tarn, 2; Brackenber Tarn, 4 (IV*d*). *Corixa panzeri*, Penmon Priory, 4 (I*e*); Mickle 5, 1 (V*e*). *C. affinis*, Penmon Priory, 1 (I*e*). *C. dentipes*, Helton Lake, 13 (III).

THE ORIENTATION AND DISTRIBUTION OF BARNACLES AT SETTLEMENT WITH PARTICULAR REFERENCE TO SURFACE CONTOUR

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(With 6 Figures in the Text)

CONTENTS

	PAGE
Introduction and terminology	142
Experimental methods	144
Experiments on the relation between rugotropism and orientation to light	145
Experiments on the orientation of *Elminius modestus* induced by grooves of different shapes	149
Experiments on the distribution of barnacles on surfaces with differently spaced grooves, pits and holes	152
Mechanism of rugophilic and rugotropic responses	158
Selection of position for setting	159
Biological significance of rugotropism	160
Acknowledgements	161
Summary	161
References	162

INTRODUCTION AND TERMINOLOGY

The results reported in a previous paper (Barnes, Crisp & Powell 1951) have shown that the orientation of the rostro-carinal axis of a number of common species of both intertidal and sublittoral barnacles is determined at settlement, and that when the substrate is plane, such as plate glass or smooth bakelite, or when its irregularities are small and randomly arranged such as ground glass, the major influence in determining the orientation is the direction of the light. The effect of water currents, if any, on such orientation was considered to be negligible under field conditions, but attention was drawn to the powerful orientating effect of grooves or other irregularities of the surface.

Evidence is now presented on the factors involved in this reaction, and on the behaviour of larvae exposed simultaneously to contact and to other orientating stimuli. The work concerns in the main two common barnacles, *Elminius modestus* Darwin and *Balanus crenatus* Brug. The observations on *Elminius modestus* were made in the Crouch at Burnham-on-Crouch, Essex, and those on *Balanus crenatus*, together with a few observations on *B. balanoides* (L.), at Millport, Scotland. There is a strong presumption, based on past experience, that many intertidal and sublittoral barnacles react very similarly to contact stimulation. The same experiments have, therefore, not been repeated with the various species, but rather an attempt has been made to bring together the evidence bearing on the problem from different types of experiment on the common species prevailing at each locality.

In considering the terms to be employed in describing the behaviour of a cypris larva during settlement, it is important to bear in mind that after migrating over one

or more surfaces it eventually proceeds, by an innate mechanism, to become permanently attached. What is observed is the pattern of orientation and distribution of those individuals which do become attached to the experimental surface; normally we have no knowledge either of those individuals which have visited the surface and swum off again, or of the prior movements of those which have settled there. The majority of terms used to describe animal behaviour—taxes, kineses and so forth—have been defined very rigidly by Fraenkel & Gunn (1940) in terms of the mechanism by which a non-sedentary animal reacts to a stimulus. Such terms are useful and avoid confusion as to the mechanism when the behaviour of an animal has been analysed fully; but they cannot be employed where only the final result of the animal's movements is known, and the mechanism is in doubt. Thus, in a previous paper we felt compelled to describe the movement of a cyprid as 'photo-positive' since we were unaware of any term for a movement towards a light source, which could properly be applied without prejudging the mechanism. Similarly, the accumulation of individuals in grooves and hollows requires a simple term which is quite neutral as to the mechanism. The term *rugophilic* (ruga = a wrinkle or groove) is suggested. Aggregation of a rugophilic animal may arise either by a directional migration along a groove, once this has been encountered, or it may be due to a general and undirected slowing down of movements whenever the cyprid enters a concavity, in either event fixation occurring more frequently in hollows (Barnes 1953). We propose to follow Fraenkel & Gunn's nomenclature in calling the former *rugotaxis* and the latter *low rugokinesis*.

Moreover, in a sessile organism, the cementing process may itself take place in response to such a contact stimulus. This could be regarded as an extreme form of low rugokinesis, but since it involves a separate fixation reaction it would be more appropriate to call it *rugostasis*. On the other hand the cementing process might be independent of the contact stimulus; it would then merely freeze such patterns as normally arise during migration over the surface.

The orientation of a given axis of the animal in the direction of the groove should be distinguished from the tendency of the animal as a whole to remain in the groove, although in rugotactic movements the two processes are associated. It is therefore useful to have a term to describe a purely angular response to a directional stimulus in the plane of the surface, independently of the mechanism by which it is acquired and irrespective of whether translation is also taking place. The term *thigmotropism*, though simple and etymologically appropriate, was introduced by Verworn (1889) in a rather different sense. We shall therefore maintain uniformity in our nomenclature by using the term *rugotropism*. Moreover, it is important to distinguish between an orientation reaction in the plane of the surface, to which the term rugotropism is intended to be applied, and an orientation reaction normal to the surface. The latter would bring the animal into the correct dorso-ventral position in relation to the surface and is obviously a very common response; for this we consider that, following Fraenkel & Gunn's nomenclature, the term *contact posture reaction* would be appropriate. The expression *selection* or *choice* of sites is frequently used in this paper to describe conveniently the fact that cyprids regularly become attached at certain positions on a surface, for example, in pits, rather

than elsewhere. The use of this expression is not intended to prejudge the mechanism by which this comes about.

EXPERIMENTAL METHODS

All the experiments consisted of exposures to barnacle settlement in the sea of surfaces possessing some uniform or regular structure. After exposure, the orientations of the settled barnacles and cyprids were measured. In certain experiments, the distribution of individuals on different regions of the exposed surface was determined by counts. The experiments fell into three main groups:

(i) Surfaces possessing a linear grain or channelling were exposed with the direction of the grain at different angles to the incident light, to compare the orientation produced by the two stimuli acting simultaneously. The effect on orientation of directional light on pitted surfaces was also examined.

(ii) Surfaces possessing grooves of widely dissimilar cross-sections were offered simultaneously to settlement in order to compare the relative orientations produced.

(iii) The density and distribution of settlement on surfaces bearing grooves, pits and holes separated by different distances, and on adjacent plane (control) surfaces was examined. These experiments throw light on the process of selection of sites by the cyprids.

In the experiments where round pits provided the contact stimulus, the vertical (0° and 180°) was taken as the reference axis as this corresponded with the direction of light, the major orientating influence present. An index of orientation was calculated by resolving and summing algebraically the individual values to give mean vertical and horizontal components, A and B respectively, as described in a prior publication (Barnes *et al.* 1951):

$$A=(\sum_i \cos \phi_i)/N, \quad B=(\sum_i \sin \phi_i)/N, \quad \theta=\tan^{-1}(B/A), \quad \sqrt{(A^2+B^2)}=R.$$

Where the grooves provided the contact stimulus, the zero axis was made to coincide with the lines of grooves. An important modification in procedure was necessary here, however, for two reasons. In the first place the orientating stimulus in the case of the grooves, though having direction, differs from that due to a light source in being without sense, that is, the intensity of the stimulus is equal in either direction. Hence an orientation of 180° is symmetrically equivalent to one of 0°, 170° ≡ 10°, etc. All orientations were therefore reduced by the following transformation to lie within a quadrant, the A axis corresponding to that of the grooves,

$$\phi \equiv -\phi \equiv \pi-\phi \equiv -\pi-\phi=\phi'.$$

By this means all components of orientation along the grooves are summed independently of sign to give a mean modulus component $|A|$, where

$$|A|=(\sum_i \cos \phi_i')/N.$$

Similarly, the orientations may be resolved into components across the grooves and made additive to give $|B|$,

$$|B|=(\sum_i \sin \phi_i')/N.$$

The significance of $|B|$ is the sum, independent of sign, of mean orientation components which lie at right angles to the grooves, and its value in relation to that of $|A|$

indicates the degree to which the individual orientations along the grooves are disturbed by other factors. Such disturbing factors might alternatively be measured as angular variances. This method was used in certain of our earlier experiments on the orientation to light where the deviations were small and apparently normal. The present method has been adopted since there is no evidence that in experiments relating to rugotropism the distribution approaches normality while the angular deviations are often large, so that a mean square deviation calculated from such data might be misleading. If the deviations, however, are small and normally distributed the two methods are related by the formula:

$$|A| = e^{-\frac{1}{2}\sigma^2} \quad |B| = \sqrt{(2\sigma^2/\pi)}\, e^{-\frac{1}{2}\sigma^2},$$

where σ, the standard deviation, is measured in radians. This relation has been derived algebraically by Dr R. A. Newing (private communication) from the definition of $|A|$ and $|B|$ given above, and the standard equation for the normal Gaussian distribution, making use of small simplifying approximations.

The second reason for a somewhat different treatment from that given in our earlier paper is due to a different approach. In the experiments establishing orientation to light it was necessary to show that the mean direction of a sample of the population coincided with that of the light; for this purpose the resultant, R, together with the mean angle θ to the supposed light axis offered the simplest description. Where the situation is similar we have again in this paper used R and θ to demonstrate orientation to light. On the other hand, the fact of orientation to grooves has never been in doubt, nor can there be any doubt about the direction of the rugotropic stimulus which is clearly along the axis of the groove. It is here solely a question of the degree of orientation which has to be considered, and the functions $|A|$ along the groove and $|B|$ across it, are therefore more appropriate than angular measurements.

EXPERIMENTS ON THE RELATION BETWEEN RUGOTROPISM AND ORIENTATION TO LIGHT

Selected pieces of wood with similar straight grain were exposed to settlement of *Elminius modestus* in the following three positions:

(*a*) With the panel vertical and the grain vertical and exposed to illumination from above so that the direction of the incident light was in the same direction as the grooves.

(*b*) With the panel horizontal and illuminated from above so that light was diffuse in all directions.

(*c*) With the panel vertical and the grain horizontal and exposed to illumination from above so that the effect of incident light was at right angles to the direction of the grooves.

The frequency distributions of orientation are shown in the histograms in Fig. 1 and the resolved components given in Table 1. On inspection of the table it will be noted that the modulus component $|A|$ is large under all conditions; this indicates that the majority of individuals are orientated parallel to, or nearly parallel to, the grooves whatever the direction of light. Light, however, still exercises an influence as is apparent from a comparison of the algebraic components A and B obtained under the

three above conditions. In the last condition (*c*) the component of orientation summed algebraically across the grooves *B*, which coincides with the direction of the light, is positive though small (0·246), whereas in the other two experiments where there was no directional light along this axis the value of *B* is small and probably insignificant

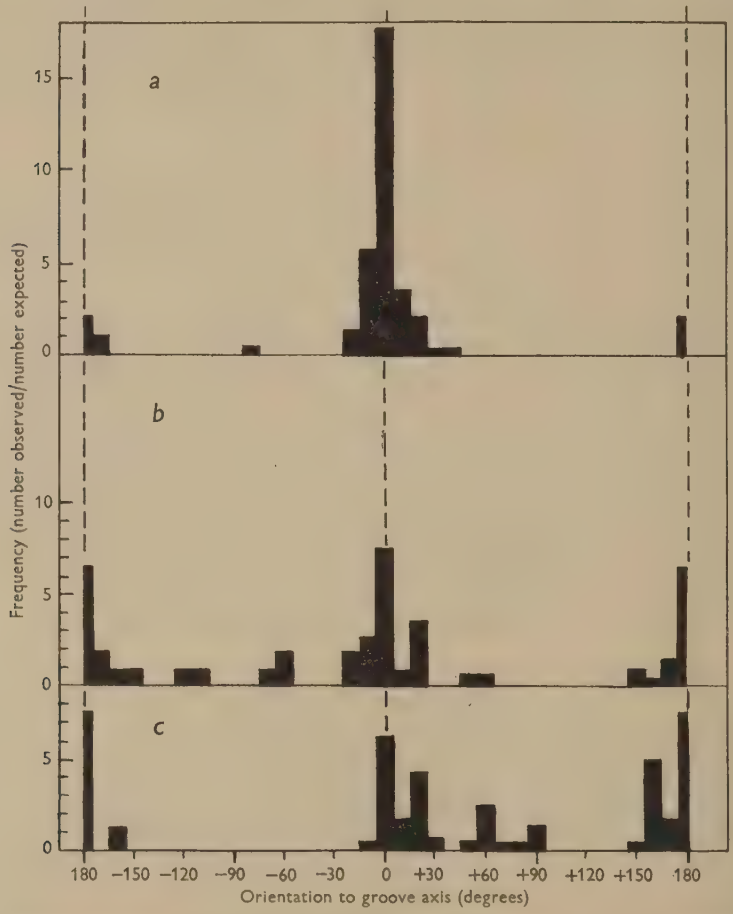

Fig. 1. Histograms showing orientation frequency of *Elminius modestus* to the grain of wood in various positions. *a*, light parallel to grain; *b*, light diffuse; *c*, light at right angles to grain. Dotted lines indicate the groove axis (0 and 180°). The frequency scale is chosen so that unity (0·278% per degree) represents the number which would be present if the orientations were uniformly distributed over 360°. The values therefore give the ratio of the number observed in a given angular range compared with random expectation.

($< 0{\cdot}10$). Similarly, the only significant value for the mean component *A* along the groove axis, is given under condition (*a*) where it again coincides with the direction of light, and is here much more pronounced than component *B* in (*c*) as the effect of light reinforces that due to the grooves. Nevertheless, so much stronger is the contact stimulus than the light stimulus that even when both coincide in direction (*a*),

a significant proportion of cyprids become attached facing away from the light, but nearly in line with the groove axis—indeed a far greater proportion than that settling across the grooves. Presumably such individuals became aligned to the grooves but facing away from the light; the light was then not a sufficient stimulus to cause them to re-orientate, for this would involve passing through a position at right angles to the grooves.

Table 1. *Components of orientation of* Elminius modestus *along grooves under various conditions of illumination*

(In all cases the zero axis (component A) is along the grooves. Where the light is at right angles to the grooves it is incident from $+90°$; where it is parallel to the grooves it is incident from $0°$. Complete orientation of all individuals would result in values of 1·0 for resultant orientation.)

	Mean components across grooves				Mean components along grooves			
	Positive	Negative	Component B	Modulus component $\lvert B \rvert$	Positive	Negative	Component A	Modulus component $\lvert A \rvert$
(*a*) Light parallel to grooves (68)	0·075	−0·066	+0·009	0·141	0·882	−0·088	+0·794	0·970
(*b*) Light diffuse (38)	0·092	−0·190	−0·098	0·282	0·514	−0·380	+0·134	0·894
(*c*) Light at right angles to grooves (57)	0·269	−0·023	+0·246	0·292	0·431	−0·443	−0·012	0·874

A similar experiment was carried out when *Balanus balanoides* cyprids were settling, but employing a slightly modified technique. Vertically suspended panels were exposed on which had been cut grooves radiating at 10° intervals from a central point. On one panel the grooves were fine scratches (0·15 mm. deep), while on the other they consisted of V-shaped furrows (0·40 mm. deep).

Table 2. *Components of orientation of* Balanus balanoides *along grooves*

(Grooves prepared radially in a 6 × 5 in. panel. Panel exposed vertically under conditions of complete submersion).

	No. in groove	No. on plane	Orientation to light: Groove R	Groove θ	Plane R	Plane θ	Orientation to groove $\lvert A \rvert$	Orientation to groove $\lvert B \rvert$
Grooves 0·40 mm. deep	9	6	0·660	−34°	0·97	− 7°	0·993	0·066
Scratches 0·15 mm. deep	24	90	0·551	+15°	0·60	−27°	0·908	0·244

The numbers settling were few and the results are given in Table 2. As in the experiments with *Elminius* on wooden panels, the major influence determining orientation of *Balanus balanoides* in both kinds of groove is the contact stimulus and not the light. This is shown by the component $\lvert A \rvert$ (taken for each individual in relation to the axis of the individual groove) which greatly exceeds $\lvert B \rvert$. Resolving the orientations as a whole to the vertical axis of the panel, it is clear that both for individuals in grooves and for those settled on the plane surface there is a tendency for them to be pointing upwards into the light ($90° > \theta > -90°$). This again indicates a tendency for orientation to be acquired towards the light in so far as is compatible with alignment to the groove.

A further series of experiments which gave additional evidence on the interrelation of light and contact stimulation were made by employing vertically placed bakelite

panels measuring 6 × 5 in. overall from which were drilled out regularly spaced pits over one half of the panel. In the first example, the pitted side contained two square patterns of pits, one below the other; the upper array contained eleven rows and twelve columns, each 0·5 cm. from the next; the pits of the lower array were 1·0 cm. apart and arranged in six rows and six columns. There were, therefore, 121 small pits on the upper half and 36 more widely spaced ones on the lower half, while opposite each array of pits was a plane (micro-rough) unpitted area of equal size. The pits in this instance were only a little larger than the cyprid of *B. balanoides*, and, being made by means of a spring punch on bakelite, were quite circular.

Panels having arrays of larger pits and with the pits more widely spaced were also prepared; in one set they were 4·75 mm. ($\frac{3}{16}$ in.) in diameter, in another they were 7·9 mm. ($\frac{5}{16}$ in.) in diameter; these pits were made by drilling and therefore were sunk slightly deeper in the centre. With the $\frac{3}{16}$ in. pits with centres 1 cm. apart, a number of the pits had accidentally been left with a small lip overhanging the edge of the pit. Just underneath this lip a ring of settled cyprids up to six in number was often found. This was a result of the strong concavity which was formed between the projecting lip and the sides of the pit.

Table 3. *Orientation and distribution of* Balanus balanoides *on pitted panels*

Diameter of holes (mm.)	Distance between centres (cm.)	Total number of holes	Number settled in holes	Number settled between holes	Number settled on adjacent surface of equal area	Orientation of individuals: In holes R	In holes θ	On plane surface R	On plane surface θ
<1	0·5	121	63	2	3	0·85	−10°	0·79	+28°
<1	1·0	36	9	3		0·68	−14°		
4·75	1·0	60	73*	34	40	0·63	− 8°	0·79	+16°
4·75	2·0	24	48	16	3	0·75	− 7°	0·86	− 9°
7·9	2·0	24	73	36	62	0·67	+ 1°	0·76	− 6°
				Mean value of $R \cos \theta$		0·708		0·770	

* A further 93 were present round the lips, on account of a defect in drilling the pits of this particular panel (see text).

Table 3 summarizes the results of counts of both metamorphosed barnacles and cyprids on these panels and their orientations, but only the observations on orientations will be dealt with in this section.

The table shows that individuals both in pits and on the plane surface are strongly orientated to the vertical, the direction from which the light was incident. Clearly the response to contact stimulution, which leads to a very great disparity of settlement in favour of the pits compared with the plane surfaces, does not influence the response to light when the pits are non-directional. The orientation in the pits is indeed very similar to that on the plane surface, although the latter series have on the whole rather larger resultants. As the orientations of those settled in pits were projected on to the plane of the panel, this in itself would tend to emphasize any disorientation so that the difference should be treated with some reserve.

There is not much variation in orientation among the different sized pits, although on the whole the barnacles in the smaller pits show better orientation than those in the

larger ones. Here an interesting point was noted on detailed inspection. In the larger pits more than one individual sometimes settled in each pit. Where this occurred and it was possible to distinguish the first to settle, or where only a single individual was present, it was invariably found that this individual was situated at the centre of the pit. These central individuals were usually well orientated to the light, but those settled later around the sides of the pit were less well orientated. This slight disorientation, which may account for the reduction in R for the larger pits, was not due to contact stimulation of one individual by another because the cyprids had 'spaced out' before settlement. Probably the annular concavity between the walls and bottom of the pit exerted contact stimulation which for some cyprids acted in a different direction from the light stimulus.

In these experiments *B. crenatus* and *B. balanoides* settled simultaneously; they have not been separated in describing the results as no difference in behaviour was apparent. For example, the first row in Table 3 gave a resultant of 0·86 and an angle of $-10°$ for *B. crenatus* and of 0·84 and an angle of $-11°$ for *B. balanoides*.

EXPERIMENTS ON THE ORIENTATION OF *ELMINIUS MODESTUS* INDUCED BY GROOVES OF DIFFERENT SHAPES

In a previous investigation it was possible to correlate the degree of orientation on a plane surface with the fraction of light falling on it in a given direction by making orientation counts and measuring the incident light over a series of angles with a photocell. Although a similar correlation of orientation with the direction of surface grooves is, in most cases, quite obvious, we cannot show the relation quantitatively as we do not at present know what feature of the groove is detected by the animal, and how it evokes the response, and hence we are unable to measure the stimulus.

Table 4. *Degree of orientation of* Elminius modestus *along grooves of different shapes*

(Types of groove: 1, Saw-cut; 2, grain of wood; 3, bevel on tile; 4, scratches on slates; 5, *Pecten* shells; 6, *Pecten* shells, control.

Type of groove	Number of individuals	$\lvert B \rvert$	$\lvert A \rvert$	Approximate radius of curvature (μ)	Approximate angle at base (°)	Approximate depth (μ)	Depth variation over 1 mm. (μ)
1	67	0·117	0·988	1000 or v. small	100 or 160	1600	1600
2	173	0·218	0·923	30–300	70–150	50–100	100
3	181	0·221	0·948	350	140	300	150
4	146	0·447	0·792	30	150	20	20
5	328	0·584	0·674	3130	—	600	43
6	334	0·628	0·614	—	—	—	—

Under field conditions there are bound to be factors which disturb the response to contact stimulation, so that the weaker the contact stimulus provided by the groove, the smaller will be the modulus component $\lvert A \rvert$ until, in the absence of any effective stimulus, both $\lvert A \rvert$ and $\lvert B \rvert$ will be approximately equal. If, therefore, we can assume that these disturbing factors are equal for the various surfaces exposed, the relative magnitude of $\lvert A \rvert$ to $\lvert B \rvert$ will be a measure of the stimulus provided by the surface. These experiments therefore consisted of exposing simultaneously a number

of surfaces with widely differing linear structures, and measuring the degree of orientation induced by each. The surface consisted of:

(*a*) Saw-cuts in bakelite panels.
(*b*) Natural grain on wood.
(*c*) Bevels on porcelain tiles.
(*d*) Scratches on slates.
(*e*) The ridges of *Pecten* shells (smooth interior surface of flat valve of *P. maximus*).

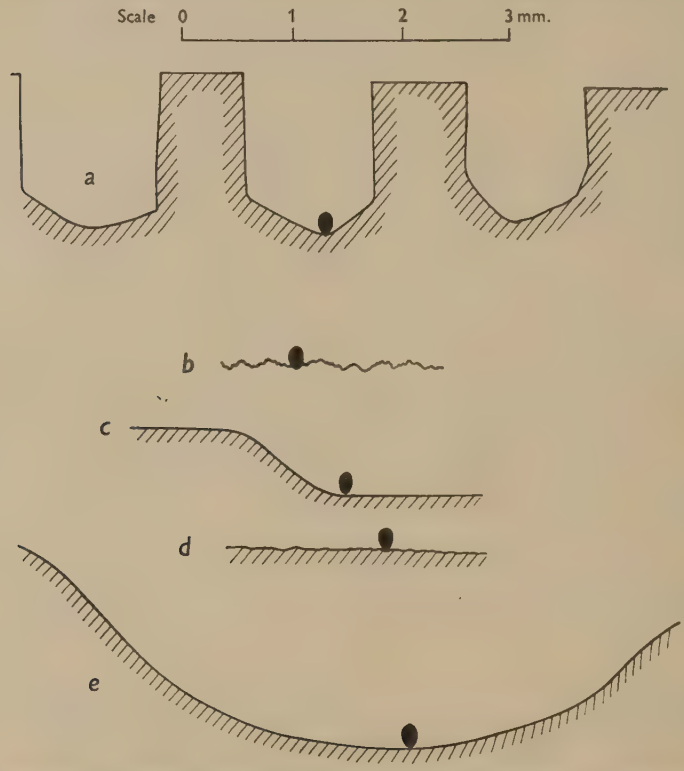

Fig. 2. Cross-section of grooves employed to determine degree of response to different shapes. A cyprid of *Elminius modestus* is shown in cross-section in each to give scale. *a*, saw-cut; *b*, natural grain of wood; *c*, porcelain tile; *d*, slates; *e*, *Pecten* shell.

In all cases the surfaces were placed horizontally where illumination was as even as possible, and, in the case of the *Pecten* shells, this was checked by counts on the flat surfaces between the grooves.

Typical sections of the surfaces used were obtained by making gelatin-glycerine or paraffin wax replicas and drawing several cross-sections of the replicas by means of a projection microscope. Fig. 2 shows these sections and includes a cross-section of a cyprid of *Elminius* of typical dimensions in each figure. Table 4 shows the resolved components, summed without regard to sense, along ($| A |$) and across ($| B |$) surfaces grooved in different ways. Column 5 shows the approximate radius of curvature at the

angle of the groove, or, in the case of the irregular wooden grooves, the best average estimate of the curvature which could be made. The radius of curvature for the saw-cuts was somewhat difficult to define, since they exhibited a gentle curve or obtuse angle at the base and a sharper angle between the base and the vertical sides. Column 6

Saw-cut
Grain of wood
Bevel of tile
Scratches on slate
Grooves on Pecten shell
Control surface
Frequency (numbers observed/numbers expected)
0 ±5 ±15 ±25 ±35 ±45 ±55 ±65 ±75 ±85 +90
180 ±175 ±165 ±155 ±145 ±135 ±125 ±115 ±105 ±95 −90
Orientation to groove axis

Fig. 3. Histograms showing orientation frequency of *Elminius* to various types of grooves. Unit frequency as in Fig. 1.

gives the angle subtended by the deepest point of the groove and the sides of the groove; it is difficult again to define for the saw-cuts, and again variable for the wooden panels and slates, average values being given in the last two instances. Column 7 gives the total depth of the grooves, and column 8 the depth of the groove measured from two lines parallel to and at a distance of 0·5 mm. from the centre line of the grooves. The significance of this measurement is that it represents the maximum distance which the cyprid, attached by the antennules at the bottom of the groove, could sweep by rotation of the body.

It will be observed both from Table 2 and from Fig. 3 that the saw-cuts give by far the most profound orientation, individuals with angles deviating from the groove direction by more than 25° being rare. The grain of softwood, which had narrow grooves about 50–100μ, and the very shallow bevel on tiles, which was up to 2 mm. in width and only very gently angled, gave comparable orientations. As might be expected, however, in view of the greater irregularity of the wood, the number of individuals at a considerable angle to the groove was greater than in the case of the tiles, while the tiles showed greater deviations close to the zero axis. The orientation pattern therefore differs significantly in detail. Finally the shallow scratches on slates produced less sharp but nevertheless significant orientations and were probably close to the limiting condition. The grooves in *Pecten* shells show a very slight tendency to orientation, but it is not convincing except in relation to the control observations.

The evidence of Table 4 is not sufficiently extensive to lead to any definite conclusion, but the results suggest that neither the angle at the base nor the radius of curvature are closely correlated with the degree of orientation. However, both absolute depth and the depth that could be directly appreciated by rotation about the antennules (that is, across a distance of 1 mm.) are well correlated with the degree of orientation observed.

EXPERIMENTS ON THE DISTRIBUTION OF BARNACLES ON SURFACES WITH DIFFERENTLY SPACED GROOVES, PITS AND HOLES

So far only observations on the orientation of barnacles on different surfaces have been considered, but the experiments described above also yield information on the distribution of barnacles over surfaces which contain special sites in the form of pits, grooves, etc. In theory the cyprids are offered a 'choice' in such an experiment between a large area of plane surface, and a number of special sites; the ratio of the density of settlement on the plane surface compared with that found simultaneously on the special sites would then afford a measure of the selectivity for the particular kind of site under the conditions of the experiment. The validity of such a ratio, however, must rest on the assumption that the sites are sufficiently close to enable the cypris larvae to exercise such a 'choice'. If the sites are too widely separated the experiments cannot then give definite evidence on the question of selection, for it may not always be certain that the larvae has 'rejected' a site from choice; its absence may simply result from no larvae having ever reached the site during its migration.

We shall therefore first describe an experiment which stresses the importance of this factor. A series of square surfaces were prepared by making saw-cuts at intervals of 6 cm. across strips of bakelite measuring 6×36 cm. Each square was then subdivided by parallel equidistant saw-cuts, the number of cuts being 0, 1, 3, 7, 14 and 29, so that the distance between the grooves was respectively 60, 30, 15, 7·5, 4 and 2 mm. These six treatments are referred to as **u**, **v**, **w**, **x**, **y** and **z**. Six strips were so treated, the order of the treatments being such that when assembled they formed a 6×6 Latin square. This arrangement has the advantage of making possible a comparison of treatments with the elimination of positional effects.

Fig. 4 gives the results of several experiments, in which the panels were placed in various positions and subjected to different intensities of settlement. Each point is an

average value obtained from six observations for each type of square, **u**, **v**, **w**, **x**, **y** and **z**. It will be seen that all experiments agree well in their main features; in other words, the settlement is not greatly influenced by the position of the panel.

The settlement is always much heavier in the grooves than on the plane surfaces though the divergence decreases with increase in total settlement. Once the grooves are full they are denied to any subsequent arrivals. Moreover, the ratio of those settling

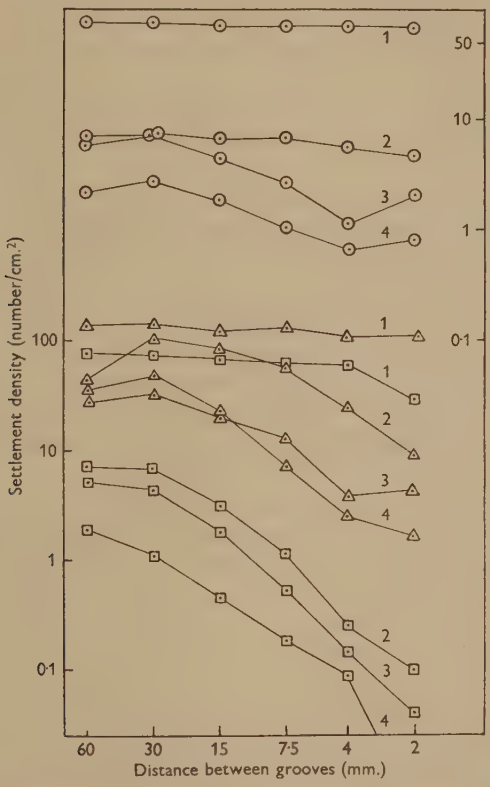

Fig. 4. Density of settlement in grooves and on plane surfaces of bakelite plotted as a function of the distance separating the grooves from each other. Both axes are for convenience reduced to a logarithmic scale. Exp. 1: panels horizontal, face down, grooves parallel to current. Heavy settlement. Exp. 2: panels horizontal, face down, grooves at right angles to current. Moderate settlement. Exp. 3: panels vertical, grooves horizontal. Light settlement. Exp. 4: panels vertical, grooves vertical. Light settlement. ⊙, Total settlement density on 36 cm.² (right-hand scale); □, density (number/cm.²) on plane surfaces (left-hand scale); △, density in grooves (left-hand scale).

on the plane surface to those settling in the grooves decreases steadily as the grooves are drawn closer together, and indeed tends to zero with the grooves 2 mm. apart. The numbers settled on the panel as a whole also decrease as more grooves are present breaking up the plane surface.

Fig. 5 illustrates the distribution of density across the plane surface between grooves 6 cm. apart. It was obtained by dividing all six squares of type **u** on each of two panels

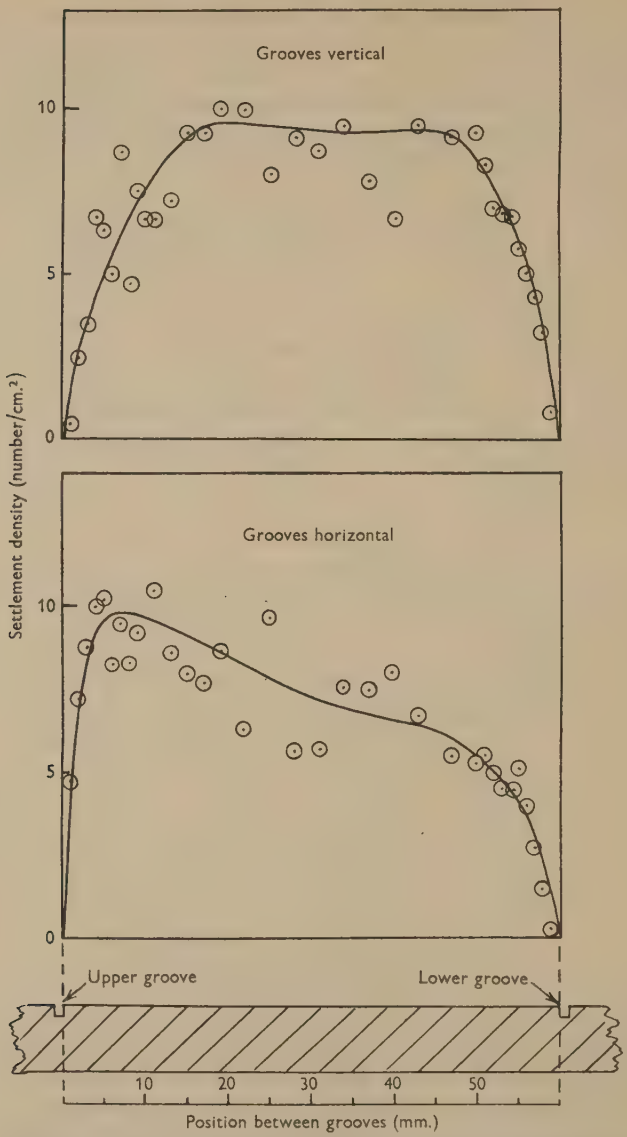

Fig. 5. Distribution of density of settlement across a plane surface between grooves 6 cm. apart. The points represent average values taken from a number of experiments.

into strips 1 mm. wide parallel to the grooves, and counting the numbers on each strip. It will be seen that the density drops rapidly towards the grooves.

These results can be interpreted as follows. When the grooves are sufficiently widely spaced, the majority of cyprids alighting on the plane surface do not find grooves at all, but as the inter-groove space decreases the chance of reaching a groove

improves until, in the case of the grooves 2 mm. apart, it is almost unity. The grooves, therefore, act as collectors of settlement, and contain more individuals when they draw them from a larger area on which settlement first occurs. Thus the grooves of the treatment **v**, with 3 cm. of plane surface between them, contain a higher density than the grooves of the **w** squares with only 1·5 cm. intervening and so on. The evidence of the distribution between the grooves (Fig. 5) corroborates these conclusions; close to the groove very few remain on the surface, while at a distance of 1 cm. or more the settlement is nearly uniform and maximal because the chances of reaching the groove before settlement takes place are remote. It will also be seen from the figure that while the distribution on the inter-groove surface is symmetrical when the grooves are vertical, it is more concentrated in the upper part when they are horizontal. This is consistent with a tendency, mentioned in our earlier paper, for migration to occur towards the light.

This upward migration is also borne out by the experiment where radial grooves were set up. Here, too, there is a great disparity between numbers settled in the grooves and the numbers on the much greater area of plane surface (Table 2). But the numbers settled in the grooves which were inclined to the horizontal axis by less than 45° were greater than the numbers in the grooves which lay between 45° and the vertical axis. While there are 24 individuals in the first group there are only 9 in the second. Comparing the numbers over a segment $\pm 10°$ from the vertical and horizontal axis the numbers are even more striking, for whereas none settled in grooves lying 10° off the vertical axis, there were 12 on the grooves within 10° of the horizontal axis.

A somewhat puzzling feature of the experiment on differently spaced grooves is the drop in total numbers when the grooves are approximated. This effect was statistically tested in well replicated experiments however. If all the cyprids alighting on the panel become distributed between the plane and grooved areas, the total settlement should not show much variation. The drop in numbers must indicate a tendency for cyprids to swim off, presumably when they encounter a groove. The grooves therefore not only lead to accumulation of settling individuals, but also cause many to be lost. The grooves were, however, deep and sharply convex at their entry from the plane surface (see Fig. 2). Perhaps on encountering this sharp angle many cyprids swam off, others entered the groove and settled there.

The experiments described above, in which pits were offered as special sites, differed from those where grooves were employed in that the accumulation of barnacles on the sites was not accompanied by the phenomenon of orientation by the contact stimulus. Nevertheless, the accumulation in the pits was very pronounced, as will be seen from the first six columns of Table 3, particularly so when the pits are close together as in the experiment described in the first row of this table. Over this particular surface more than half the pits were occupied by a barnacle settled neatly in the centre, while only two individuals were found on the flat surface between the pits. It is reasonable to suppose that the pits are always 'preferred', and that the two individuals found on the flat surface had by chance never encountered a pit. This conclusion is supported by the data for the adjacent square, where a greater proportion of cyprids were found on the plane surface, as the pits (identical in form) were more

widely spaced. Considering the size of the cyprid, and the consequently narrow path it must explore, either the migrations over the surface must be very extensive, in order to find so high a proportion in these minute pits, or else many cyprids which fail to enter a pit soon after arrival must swim off again. Moreover, there is a great disparity between the numbers on the pitted side and the numbers on the control half evident throughout the whole experiment. Clearly equal numbers will settle by chance on both halves. The difference must arise, therefore, either because those alighting on the plane half migrate to the other side and settle there, or because many alighting on the plane half are not stimulated to settle and so swim off again. It seems unlikely that the cyprids of *Balanus crenatus* settling on the control half migrate so extensively that they explore the whole panel, and thus find pits, especially if they tend to move upwards (see below). Therefore the sparse settlement on the control half is on account of the fact that the majority do not encounter a pit and, after an unsuccessful migration swim off again. In the *Elminius* experiment, using spaced grooves, there was a heavier settlement density and a considerable proportion of barnacles settled fairly readily on the plane surface. But in both experiments cyprids which might otherwise have swum off again or settled on the surrounding plane surface were induced to settle in high density in grooves or pits by the rugostatic stimulus.

The tendency for the cyprids on a vertical panel to move upwards towards the light, and to accumulate in a groove, or in the case of a plane panel at a 'neutral area' where the shade of the panel support terminates the light gradient, was generally obliterated by the presence of pits. On such surfaces there was little or no upward bias in distribution and the settlement was very uniform. For example, in the first experiment of Table 3 there were in the upper five rows 5·4 individuals per row, and in the lower six rows 6·0 individuals per row. This uniformity can only imply that the cyprids do not continue to move upwards after they have encountered a discontinuity; indeed it is most probable that they remain and settle in the pit forthwith. There is therefore no evidence here that a pit or groove which would be ineffective at the beginning of migration over the panel would evoke a response later in the migration when the cyprid had moved upwards towards the light. This evidently suggests that the cyprid normally responds to the first pit or not at all. If so there is no lowering of the threshold of response during a given surface migration.

In order to ascertain further the cause of settlement in pits, an essentially similar experiment was carried out in which the panels were perforated by holes, the drillings being taken through the panel instead of ending blindly as a pit. This was exposed to settlement in order to indicate whether the discontinuity of the surface alone was responsible for stimulating settlement. However, cyprids were not found accumulated around or near the holes (except at occasional 'burrs'), nor were there in general greater numbers settled on 'holed' panels compared with adjacent plane surfaces. In this respect the result was therefore clearly negative.

The orientations as would be expected were similar on holed and plane surfaces, light being the orientating influence on both. For example with $\frac{3}{16}$ in. holes, centres spaced at 2 cm. apart, the orientations on the 'holed' sides were: $\theta = 10°$, 19°; $R = 0{\cdot}58$, 0·77; while on the control sides $\theta = 19°$, 17°; $R = 0{\cdot}61$, 0·77.

In one experiment (scheme B, Fig. 6) the holes were large (8 mm.) and placed 2 cm.

apart in staggered rows 1 cm. above one another, while in another (scheme A) they were smaller (4·7 mm.) and placed in a square pattern 2 cm. distant each way. Fig. 6 shows the arrangement of holes in each experiment and the distribution of settlement. The results show that the larger holes caused a reduction in total settlement. Furthermore, the tendency of cyprids to accumulate at the top of the panel was well marked in the controls and in the panel with small holes, but was practically eliminated in the panel with the larger staggered holes.

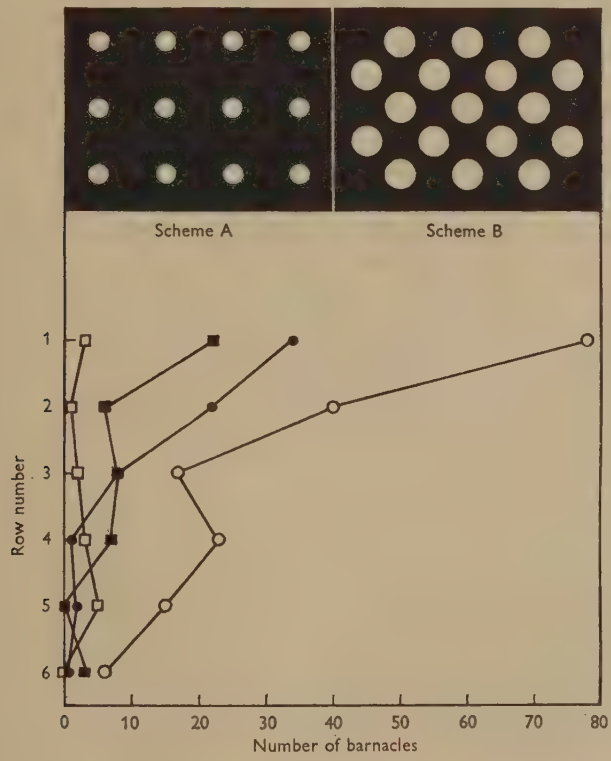

Fig. 6. Effect of holes on the density of settlement on vertical panels. Circles, scheme A: ○, between holes; ●, adjacent control panel without holes. Squares, scheme B: □, between holes; ■, control.

These results, though on a very limited degree of replication, are closely in conformity with the behaviour suggested above. The cyprids appear to move upwards and accumulate towards the upper edge of a panel unless they meet an obstruction. If this obstruction is a hole, the cyprid tends to swim off. Thus in the experiment with small holes few cyprids would encounter them while migrating up, but with the larger staggered holes the chance of migrating 2 cm. or more upwards was remote, and the residual settlement was therefore very low in comparison. Detailed inspection of the top of the panel with small holes where settlement was fairly dense, showed a tendency for fewer cyprids to be present immediately above a hole.

THE MECHANISM OF RUGOPHILIC AND RUGOTROPIC RESPONSES

Under static conditions in the laboratory cyprids show the same tendency to settle in hollows and to align the body to grooves that they show in the sea (Knight-Jones & Crisp 1953). They are therefore not made aware of the contour of the surface by water movements and eddies, developed as a result of such contours, nor do they settle in hollows on account of the shelter afforded from prevailing water currents. Such a mechanism would in any case be most improbable, for the size of grooves which can be detected would in some instances scarcely disturb laminar flow over the surface—as shown by the small value of Reynolds number R, under such conditions. For example, if the external water velocity were 100 cm./sec., viscosity 0·01 poise, density 1 g./c.c., and the height of the discontinuities of the order of 20μ, $R=20$, which is far below the critical value for turbulence. Nor can the response to grooves be ascribed to the established response of the cypris larva to light. In a deep groove light is restricted by the walls, but allowed to pass along the length of the groove so that rugotropic and rugotactic responses might be attributed to the pattern of illumination. This, however, would scarcely account for orientation in very shallow grooves 20μ deep (e.g. on slates in Fig. 2) where the cyprid eye is actually at a higher level than the tops of the ridges. Furthermore, the experiments in which both directional light and surface grooves were allowed to affect the larvae simultaneously showed clearly that both factors operated independently but that the dominant response was to the grooves rather than to light. It can therefore be concluded that the rugophilic and rugotropic responses are elicited directly by the shape of the surface and are dependent upon a tactile sense.

A wide variety of shapes and sizes of groove, both much smaller and much larger than the cyprid, can cause orientation. This suggests that the reaction is not simply one whereby a maximum contact between the body and the substrate determines the position, but rather one which involves a much finer appreciation of the contour of the surface. The observations here are consistent with the hypothesis that the main factor to which the cyprid responds is the depth of the groove which can be appreciated across a distance of about 1 mm. and that such a response could be obtained by the cyprid swinging its posterior end in a horizontal plane while pivoted by the antennules. The hind end is furnished with fine setae which can be protruded postero-ventrally between the bivalve carapace, while the antennules themselves would enable a proprioceptive recognition to be obtained during the walking phase. Thus if the deepest part of the groove were simultaneously located by the anterior and posterior end the animal would be able to orientate along the groove without difficulty.

The experiments in which a stimulus due to light was directed at right angles to the axis of the grooves and thereby produced a modification of the rugotropic effect towards the illuminated side, offers some hope of measuring quantitatively the stimulus afforded by grooves of different shapes by adjusting the gradient of light to produce a given mean deflexion from the groove axis. There are few records in the literature where attempts have been made to compare the relative sensitivity of an organism towards two different kinds of stimulation by applying them in opposition or at right angles to each other. Chance & Smith (1946) have compared the illumination required

to counteract geotropism in the root of *Fagopyrum* seedlings by this means. Fitting (1937*a*, *b*) has shown that the dorso-ventral axis of liverworts can sometimes be reversed by illumination from below and by this means demonstrated that in *Marchantia* the response to gravity overshadowed that due to light, while in *Lunularia* light exercised the greater effect. There was also a weak contact response, but the effect of this, contrary to expectation, was to induce a dorsal surface and was therefore in nature always dominated by the orientating effects of both light and gravity.

The orientational (rugotropic) and the setting (rugostatic) responses are clearly independent, for setting is promoted by circular pits which do not have any orientating effect as well as by grooves which cause orientation. Without directly observing the behaviour it is not possible to establish whether setting in grooves is preceded by rugotaxy—the animal walking along the groove once it has encountered it and finally settling in it—or whether settlement is due to low rugokinesis, a tendency for movement to be inhibited once a groove has been entered. It seems probable on general grounds that the cyprid aligns itself in the course of rugotactic movements, but it is clear from the efficiency of circular pits in causing settlement that once a suitable concavity is reached rugostasis can take place at once and that a phase of rugotactic movement is not an essential part of the pattern of behaviour.

Cyprids migrating over a plane surface may leave the surface unless they encounter a concavity which stimulates setting and metamorphosis. It is not possible to give an accurate value for the mean length of path traversed by a cyprid before swimming off again; it may vary greatly with conditions. The experiments with spaced grooves (p. 152) show a falling off in numbers up to 1 cm. from a groove suggesting a minimum order of magnitude of 1·5–2·0 cm. for cyprids of *Elminius modestus*, while the experiment where large staggered holes greatly reduced setting indicates a similar value for *Balanus balanoides* and *B. crenatus*. If, however, the tracks are curved or spiral, much greater linear distances may be covered. It is quite certain that cyprids must alight and swim off exposed surfaces with much greater facility than has hitherto been supposed. As a result surfaces are on an average very thoroughly explored by cyprid populations in the course of settlement under natural conditions, and this accounts in part for the remarkable way in which favourable positions such as grooves and hollows are colonized before any appreciable settlement occurs on surrounding plane surfaces.

There is also evidence of a converse effect, the greater tendency for cyprids to leave the surface at ridges and convexities. This is the only satisfactory explanation for the low settlement observed on panels with numerous ridges and grooves and on panels with holes (p. 155).

SELECTION OF POSITION FOR SETTING

Experiments with grooves and pits separated by various distances show that if such sites are placed less than 5 mm. from one another the cyprids are able to find them by exploration, whereas if they are placed farther apart, then they may not be accessible to all the migrating larvae and a few which do not encounter them may therefore settle on the plane surface. In practically all experiments where the favourable sites were accessible they were occupied first. In this process of 'selection' there arises an

important distinction in behaviour. The cyprid might, on entering a pit, remain there as a result of an automatic response to contact. On the other hand, it might enter and crawl out from several pits in turn in the course of its exploration and then enter one of them and metamorphose. The latter process, involving a measure of true selection, and indicating some degree of perception of surface contour, would represent a much more advance behaviour than the former. In order to account on the former hypothesis for the fact that the less favourable sites are occupied in the course of settlement after the more favourable ones have been colonized, it would be necessary to add a further supposition that a reduction of the threshold of stimulation takes place on the part of cyprids attaching to the surface later. There are two pieces of evidence which make this a tenable suggestion. First, such a reduction in the threshold of stimulation has been shown to occur in the larvae of *Spirorbis borealis* (Knight-Jones 1953) if they are artificially prevented from setting after liberation. Secondly, in *Elminius modestus* and other barnacles, according to Knight-Jones & Stevenson (1950), and in *Spirorbis* (Knight-Jones 1951), contact with adult or spat of their own species causes a marked lowering of threshold for stimulation of setting reaction so that a great increase in setting rate occurs after initial attachment (Knight-Jones & Crisp 1953).

Most of the results recorded in this paper can be interpreted on the basis of this simple behaviour, but one or two isolated observations suggest that cyprids may on occasion be able to discriminate between sites and choose the more favourable. In the experiment where larvae entered large pits (p. 149) they were observed to occupy the centre position first, but subsequently when the centre position was occupied others set in the slightly less favourable sites at the base of the wall of the pit. Since the first ones when crawling into the centre must have passed over and out of sites occupied by those entering afterwards they must then have exercised some degree of true selection. Similarly, in the experiment where panels bearing numerous parallel grooves were placed adjacent to a plane area 6×6 cm. (p. 152) the groove adjacent to the plane surface usually bore the heaviest settlement, but the one or two adjacent to it also had significantly more spat than average showing that the cyprids occasionally wander into and out of several grooves before setting in one. Clearly this point is best resolved by direct observations.

BIOLOGICAL SIGNIFICANCE OF RUGOTROPISM

The advantage to an organism which must withstand wave action of cementing itself to a rough rather than a smooth surface is self evident. It has been observed that a greater number of individuals of *Balanus balanoides*, *B. crenatus* and *Elminius modestus* are lost from growths on smooth glass than from frosted glass surfaces; in the second species the whole of the calcareous base may come away from a smooth glass plate but not from a frosted surface. It is clear, therefore, that settlement in a small hollow (rugophilic reaction) is advantageous, ensuring both an initial key for the cement and some measure of protection to the young barnacle. The need for rugotropism is rather less obvious, however, for there is no reason to believe that the adhesion of the adult barnacle would be influenced by its orientation in relation to the ridges and grooves, although the newly metamorphosed barnacle might be more firmly cemented and better protected in a groove of about its own cross-section, if it were longways on. However, the

response is considerably more sensitive than is demanded by this contingency as it promotes orientation in scratches much smaller than the cypris. Possibly the ability to orientate to large grooves requires a mechanism very sensitive to contour and this is manifested in the response to very small grooves. It is also possible that the cyprid migrates along a scratch, since there is a greater likelihood of reaching a larger groove by following a fissure than exploring at random, but if it does not reach a wider groove it settles in the scratch orientated along it. Certainly some degree of rugotaxy occurs, for in long deep grooves the accumulated settlement is 'spaced out' just as it is in a dense two-dimensional settlement on a plane surface; this spacing out must involve adjustment of the setting position by wandering along the groove. In some pedunculate barnacles the complemental males are orientated rugotropically by the fissures of the compartments of the host individual (see Barnes 1953). The males of such species are secondarily reduced and have probably retained the response to surface contour, though it is not known to what extent this reaction is typical of cyprids of the Lepadidae in general.

ACKNOWLEDGEMENTS

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SUMMARY

1. Cypris larvae of *Balanus balanoides*, *B. crenatus*, and *Elminius modestus* settle in grooves and concavities, a tendency which we have termed *rugophilic*. If the concavity is a groove, rugophilic settlement is usually characterized by *rugotropism*, an orientation of the antero-posterior axis of the animal to that of the groove. There is some evidence of the converse effect, namely, for cyprids to swim off at sharp convex angles and ridges.

2. Rugotropism is shown to be a tactile response to surface contour.

3. Orientation to light and to surface contour are independent reactions. When the larvae are subjected to both stimuli simultaneously they react to both, but the response to contour appears generally to be the stronger. When they settle in round pits, they orientate to light just as they do when setting on a plane surface.

4. Cypris larvae can orientate along grooves much smaller than or considerably larger than their own size. It is suggested that rotation about the antennules at the time of setting enables the cyprid to appreciate the direction of the groove.

5. Migration into grooves results in a reduction in the number settled on the surfaces immediately next to the groove. If subjected to prolonged or heavy settlement, these surfaces also become covered with spat after the grooves are crowded.

6. Settlement on plane surfaces tends to accumulate towards the more strongly illuminated side. This tendency is reduced on surfaces containing many pits or grooves, since these stimulate settlement, and also by surfaces with holes which interfere with migration towards the light.

7. The larvae explore surfaces very extensively before setting, the first to settle usually having located the concavities. It is not known to what extent this prior

occupation of favoured sites is evidence of true selection, or whether later attached cyprids, denied the better sites, then undergo a lowering of threshold of the setting reaction and settle elsewhere.

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RECENT CHANGES IN THE DISTRIBUTION OF THE INTERTIDAL BARNACLES *CHTHAMALUS STELLATUS* POLI AND *BALANUS BALANOIDES* L. IN THE BRITISH ISLES

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(With 7 Figures in the Text)

INTRODUCTION

The two commonest species of intertidal barnacles indigenous to the British Isles* have very different geographical distributions, and belong to different faunal groups. *Chthamalus stellatus* Poli is a Tropical-Lusitanian form which reaches its northern limit in Scotland, while *Balanus balanoides* L. is a Boreal-Arctic form which reaches its southernmost European limits in south-west England and northern France. Over a large part of the British Isles the two species occur together, but *Chthamalus* is dominant in the south and west while *Balanus* alone is present in the north and east (see Darwin 1854, pp. 272 and 456). Since both *Chthamalus stellatus* and *Balanus balanoides* are at the limits of their respective distributions in the British Isles, these limits may be particularly sensitive to any general change in the environment. Such a change might also affect many other organisms, and will well repay careful study.

THE CHANGES IN THE DISTRIBUTION

It was in 1949 that we first suspected that there might have been comparatively recent changes in the distribution of these barnacles in the British Isles. In that year one of us discovered *Chthamalus* in the Isle of Man (Southward 1950), while the other found it at St Catherine's Point, Isle of Wight, farther east on the English side of the Channel (Crisp 1950) than suggested by previous accounts of its distribution (Moore & Kitching 1939). Further investigations by both of us (Crisp 1950, Southward 1951) showed that *Chthamalus* was present practically all round the Irish Sea. Unfortunately, the previous records for this area are both scanty and conflicting (Darwin 1854, Marrat 1886, Moore & Kitching 1939), and part of the apparent spread in the area may be a result of the more intensive nature of the recent investigations. Furthermore, *Chthamalus* is now known to have been present on the coast of Co. Down, Northern Ireland, in 1938 (Williams 1950), while a photograph taken in the Isle of Man in 1932 has come to light, showing what is undoubtedly a single specimen growing at H.W.N. However, more recent investigations, briefly reported in *Nature* (Southward & Crisp 1952), show that a real change in the distribution has taken place, *Balanus* having apparently retreated from its southern and western limits, while *Chthamalus* has advanced. Decisive evidence for this has been obtained from three localities, and is supported by confirmatory evidence from several other regions.

* The immigrant Australasian barnacle *Elminius modestus* Darwin is now as common as, or commoner than, *Balanus* on parts of the coast of southern England and the Irish Sea.

(*a*) *The Plymouth Area*

Preliminary observations at Tinside in 1950 (Southward 1951) indicated a considerably lower proportion of *Balanus balanoides* in the barnacle population than that described by Moore (1936). In 1951 the opportunity was taken to re-investigate completely the places worked by Moore in 1934. The places were: Amory Bight, between Rame Head and Penlee Point; Misery Point, just within the estuary of the River Yealm; Tinside, just below the Laboratory; and Hen Point up the Hamoaze, near Saltash. The station on Drake's Island was omitted. At each locality, several counts were made at every 0·6 m. (2 ft.) down the intertidal zone on areas of 100 or

Table 1. *Distribution of barnacles in the Plymouth area in September 1951, as numbers per square metre*

(To be compared with the tables in Moore (1936, pp. 711–15). The levels were measured from a fixed point on the shore; at Tinside the fixed point was referred to the nearest benchmark of the Ordnance Survey; at the other stations its height was estimated by reference to the predicted height of the tide at the time.)

	Level, in metres relative to Ordnance datum	*Chthamalus stellatus*	*Balanus balanoides*	*Balanus perforatus*	*Balanus crenatus* and *B. improvisus*	*Elminius modestus*
Amory Bight, 16 Sept.	4·5	0	—	—	—	—
	3·9	450	—	—	—	—
	3·3	2,200	—	—	—	—
	2·7	67,600	—	—	—	—
	2·1	75,200	—	—	—	—
	1·5	73,600	—	—	—	—
	0·9	78,120	—	—	—	—
	0·2	44,400	—	—	—	—
	−0·4	23,400	—	—	—	—
	−1·0	15,500	—	—	—	—
	−1·6	9,600	—	—	—	—
	−1·9	0	—	200	—	—
Misery Point, 8 Sept.	2·7	4,500	—	—	—	—
	2·1	46,800	—	—	—	—
	1·5	41,200	1	—	—	—
	0·9	73,600	—	—	—	—
	0·3	30,000	—	—	—	—
	−0·3	21,200	—	—	—	—
	−0·9	766	—	300	—	—
	−1·5	0	—	200	—	—
Tinside, 2 Sept.	2·28	500	—	—	—	—
	1·67	28,840	—	—	—	—
	1·06	32,400	—	—	—	—
	0·45	30,800	—	—	—	—
	−0·16	24,000	—	—	—	—
	−0·77	19,600	—	—	—	—
	−1·38	1,150	—	100	—	—
	−1·68	0	—	200	—	—
Hen Point, 4 Sept.	1·4	200	—	—	—	—
	1·1	550	—	—	—	—
	0·4	400	66	—	—	2,333
	0·2	0	500	—	—	25,600
	0	—	75	—	—	28,200
	−0·2	—	400	—	400	9,600
	−0·7	—	0	—	5,200	8,800
	−1·9	—	—	—	1,800	18,800
	−2·4	—	—	—	23,200	9,600

25 cm.^{2} according to the density of the barnacles (Table 1). The numbers present were then compared with those found by Moore, who used a similar counting technique, but who also determined the relative weights of dry tissue (the latter technique was not feasible for the present investigations).

As Fig. 1 shows, *B. balanoides* was almost absent from the Plymouth area in 1951, whereas in 1934 it had constituted at least half of the total barnacle population. A few specimens were seen at Tinside and Misery Point, but insufficient to be shown on the diagram. Even in caves and under overhanging rocks, apparently the most favourable situations, the numbers of *Balanus* did not exceed 700/m.^{2}, compared with up to 12,000 *Chthamalus*/m.^{2} in the same places. *Balanus* was somewhat commoner up the Hamoaze and at Phoenix Wharf, but even in these sheltered situations the numbers

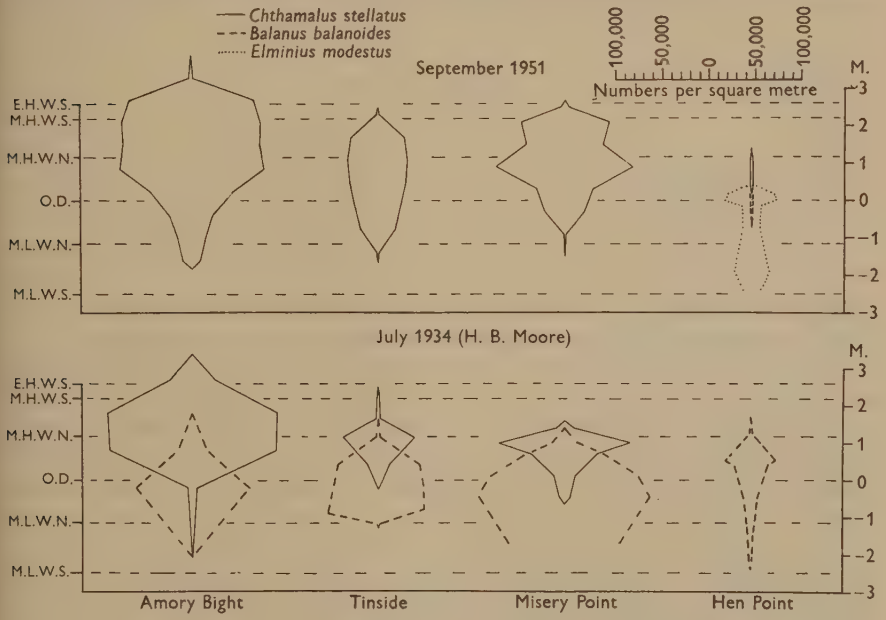

Fig. 1. Distribution of barnacles in the Plymouth area in 1934 and 1951.

were much reduced. In fact at both Hen Point and Phoenix Wharf *Elminius modestus* was much commoner than *Balanus*, which it appeared to have replaced to a large extent (Fig. 1). At the other stations the gap left by the decline in *Balanus* appears to have been filled almost completely by *Chthamalus*, for the total barnacle populations in 1934 and 1951 were very little different.

Observations at Tinside and Wembury support the view that the change has been comparatively recent. For example, at Tinside samples of *Balanus balanoides* (for estimation of the infection by *Hemioniscus balani* Spence Bate) were taken without difficulty in 1950, but in 1951 a further estimation was impossible because so few adult specimens could be found. At Wembury it appears that *Balanus* was present in some number in 1946 (Dr R. G. Evans, personal communication); in 1950 very few specimens could be found, and in 1951 only two were seen in an hour's search of Church Reef.

(*b*) *Brixham, south Devon*

Observations at Brixham were made at Shoalstone Beach, an exposed north-facing limestone and sandstone shore on the south side of Torbay. Table 2 shows the results of counts made in 1949 and 1952. At each tide-level about fifty random counts of the numbers per square centimetre were made, with the aid of a glass grid marked in centimetres. The results have been converted to numbers per square metre for comparison with the other observations. There was clearly a marked reduction in the

Table 2. *Density of* Chthamalus stellatus *and* Balanus balanoides *at Shoalstone beach, Brixham*

	1949		1952	
	Balanus	*Chthamalus*	*Balanus*	*Chthamalus*
M.H.W.S.	—	—	0	4,300
M.H.W.N.	16,900	27,600	2,500	54,900
M.T.L.	19,800	26,400	4,500	28,000
M.L.W.N.	20,000	1,500	3,500	21,000
Means				
All levels, vertical surfaces	20,100	14,000	5,400	34,500
All levels, horizontal surfaces	17,700	23,000	1,600	34,800
All levels, all surfaces	18,900	18,500	3,500	34,600
Grand mean	37,400		38,100	

numbers of *Balanus* and a corresponding increase in the numbers of *Chthamalus*, for in 1952 *Balanus* constituted less than 10% of the barnacle population, whereas in 1949 it made up about half of the total barnacle population. As at Plymouth, these changes were especially marked at the lower levels. Also as at Plymouth, the total barnacle population remained remarkably constant, although the ratio of the two species had altered considerably. Thus, *Chthamalus* again appears to have filled in the niches where *Balanus* disappeared. The change in population at Brixham was so marked that whereas in 1948–49 it was possible to collect *B. balanoides* at random, even at H.W.N., by the end of 1951 it was difficult to obtain an adequate sample of reasonably large individuals. However, in the shelter of the outer harbour, only a few hundred yards away, *Balanus* has remained common. Conditions there seem to be unsuitable for *Chthamalus*, since few spat settle in summer when abundant settlement occurs outside.

The observations at both Plymouth and Brixham bear out a general tendency (previously noted by Hatton & Fischer-Piette 1932) of *Balanus balanoides* to favour embayed situations. As the habitat becomes progressively less favourable towards the south-west, the species becomes more and more closely restricted to such embayed situations, first to sheltered bays, then to harbours, and finally to estuaries. Thus, in south Cornwall in 1950 there were no *Balanus* on the open coast, but a few individuals, chiefly spat, were to be found in the estuaries, as for example the Helford river at Porth Navas. Farther west, however, the species was completely absent, even for example in the shelter of Penzance Harbour. The retention of residual populations in sheltered sites is important in making possible a restoration of the open coast population, should conditions there become favourable again.

(*c*) *North Devon and Cornwall*

On the northern coasts of Devon and Cornwall, the barnacle populations appear to have undergone changes similar to those on the southern coasts of these counties. Thus, at Millook Haven, North Cornwall, Moore & Kitching (1939) recorded *B. balanoides* as constituting 12% of the barnacle population in 1934; in 1951, at Trevone, North Cornwall, only two specimens were seen in half-an-hour's searching. Similarly, at Westward Ho!, North Devon, barnacle samples taken during 1949 usually contained up to 5% *Balanus*, the rest being *Chthamalus*, but in 1951–52 it was impossible to obtain an adequate sample of *Balanus*. Mr E. Norris (personal communication) confirms that in the winter of 1951–52 scarcely any *Balanus* could be found along this stretch of beach. In Croyde Bay, where the species was rare in 1949, it was entirely absent in 1951.

(*d*) *The Isle of Man*

As noted previously (Southward 1950), the records of *Chthamalus* in the Isle of Man are rather conflicting. Darwin's (1854) record cannot be traced to any of the local literature, and appears to have been communicated privately by Prof. E. Forbes; Marrat's (1886) habitat ('tide-pools') is a doubtful one for *Chthamalus*, but it does seem to have been present in 1932, in spite of Moore & Kitching's (1939) absence record, though it is not possible to determine whether there has been any increase since then. However, the species has certainly increased since 1949, and at the same time the population of *Balanus balanoides* has shown considerable fluctuations. This is clearly brought out by quantitative observations made every year since 1949 on an area of limestone rock at Port St Mary, on the east coast of the island. The area has been accurately surveyed and contoured, and by means of sample counts at each foot contour along a series of marked traverses quantitative maps of the distribution have been prepared. The distributions of the two species of barnacles are shown separately on Figs. 2 and 3. In the case of *Chthamalus* the counts were made on areas of 1 m.^{2}, but for *Balanus* on several areas of 100 cm.^{2} at each level. It is obvious from the maps that the population of *Chthamalus* was practically doubled between 1949 and 1951 (unfortunately *Chthamalus* was not counted in 1950) and that there was a smaller increase between 1951 and 1952. At the same time the species showed a tendency to spread farther down the intertidal zone, a tendency as significant as the numerical increase in demonstrating the increasing favourability of the habitat. During the same period *Balanus* declined, the numbers present in 1951 being only half of those found in 1949; the decrease was particularly noticeable towards high-water neaps. However, a more successful spat-fall occurred in the spring of 1952, and by the autumn the numbers present were about three-quarters of the 1949 population (Fig. 3).

(*e*) *The British Isles as a whole*

In addition to the foregoing evidence, we have made quantitative observations on *Chthamalus stellatus* and *Balanus balanoides* at many other places in the British Isles, and are in a position to make a comparison of the present distribution with that in the 'thirties, as described by Moore & Kitching (1939). Unfortunately many of the

earlier records are quantitatively vague, and we have had to assume that 'present' can mean anything up to 25% of the barnacle population, 'plentiful' and 'abundant' anything up to 50%, and 'commoner than *Balanus*' over 50% where these statements are applied to *Chthamalus*. It is also difficult to relate the figures for percentage composition of the barnacle population given by Moore & Kitching with the percentages of the present work. The former are derived from the relative weights of dry tissue of

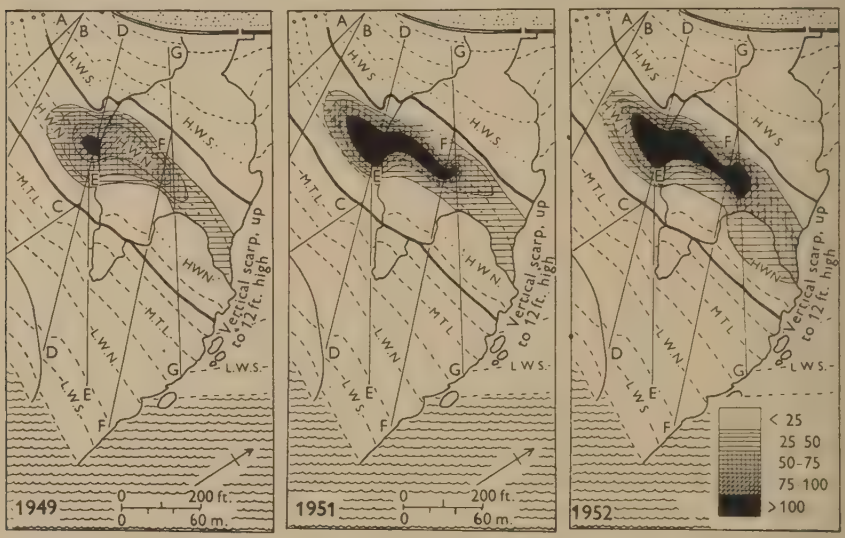

Fig. 2. Numbers per square metre of *Chthamalus stellatus* at Kallow Point, Port St Mary, Isle of Man. The thick line indicates the extreme limits of the species.

each species per unit area, while ours are based on numerical counts only. The differences may not be so great, since the size of each of the two species usually shows a similar relation to the environment; e.g. where *Balanus* grows bigger, and is therefore less numerous, *Chthamalus* also tends to be larger and less dense. Fig. 4 compares the relative distributions of *Balanus* and *Chthamalus* in the 'thirties and to-day, as percentages of the total barnacle population at each place. In spite of the above reservations, there does appear to have been a general increase in the proportions of *Chthamalus* and a decrease in the *Balanus*, but the change is much more obvious in the south and west, where the recent detailed observations are also conclusive.

POSSIBLE CAUSES OF THE CHANGES

There are several factors which have undergone changes concurrently with the observed changes in the distribution, and which may therefore be considered as possible causes of these changes.

(*a*) *Biological*

We can dismiss, almost at once, the effects of the recent encroachment of the immigrant barnacle *Elminius modestus*, which is rapidly replacing *Balanus balanoides* on many parts of the south coast of England, since in the south-west *Elminius* is rarely

found outside the estuaries, yet it is upon the open coast that the greatest depletion of *Balanus* has occurred. However, the replacement of *Balanus* by *Elminius* in sheltered places in south-west England would clearly be accelerated by any change which operated unfavourably to *Balanus balanoides*.

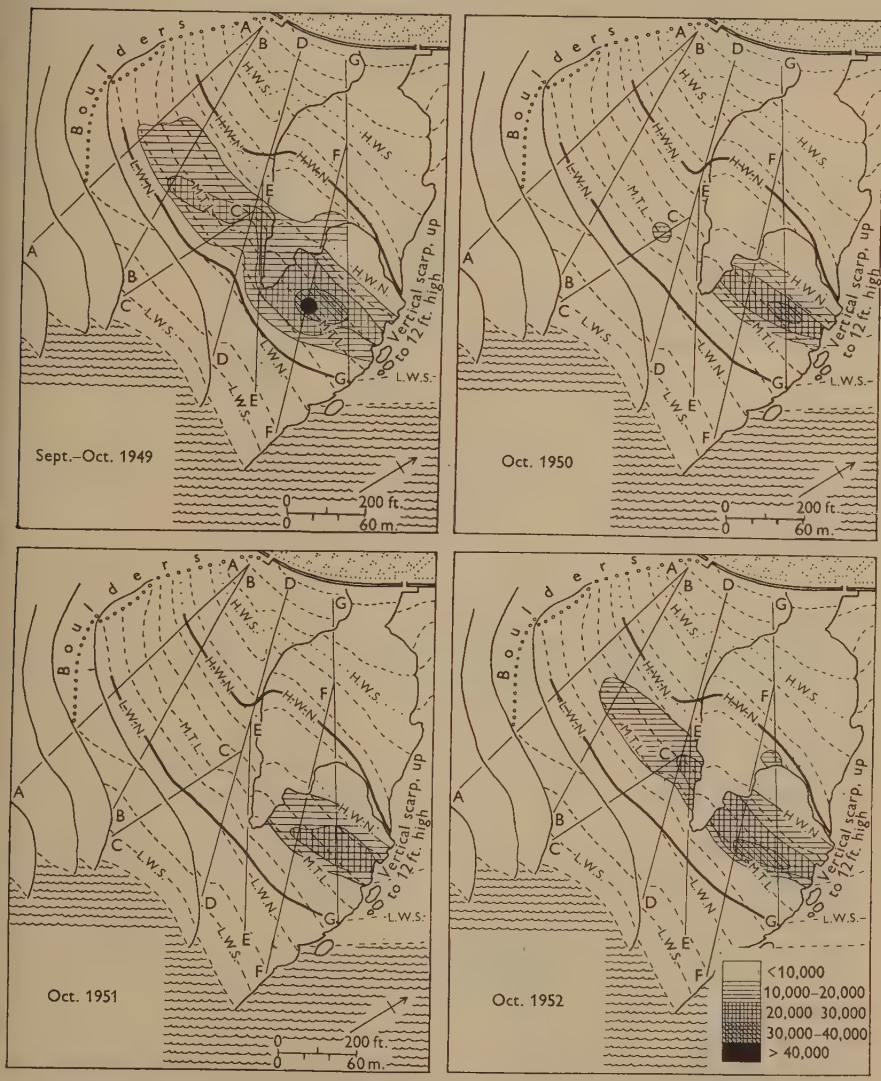

Fig. 3. Numbers per square metre of *Balanus balanoides* at Kallow Point, Port St Mary, Isle of Man. The thick line indicates the extreme limits of the species.

The sterilizing effect of the parasitic Isopod, *Hemioniscus balani*, on *Balanus balanoides* may be more important. The incidence of this species, which lives in the mantle cavity of the barnacle and partially or completely reduces the fecundity of the host,

Fig. 4. The relative proportions of *Balanus balanoides* (white) and *Chthamalus stellatus* (black) at places round the British Isles: (*a*) 1932–38, based on Moore & Kitching (1939); (*b*) 1949–52, means of counts at all tide levels: stations bearing a question mark not fully quantitative.

increased markedly in the south-west of England between 1949 and 1951 (Table 3). *Hemioniscus* does not attack *Chthamalus*, at least not in the British Isles, but *Elminius* is usually infected to the same degree as *Balanus* (Crisp & Molesworth 1951). Thus *Elminius* could provide a reserve host for the parasite permitting a high incidence in the normal host *Balanus*, even to the point of extinction. At the same time the more

Table 3. *Observations on the infection of* Balanus balanoides *by* Hemioniscus balani *in south Devon and Cornwall*

		Number of *Balanus* examined	% infected
Brixham	Winter 1948–49	3402	9
Brixham	December 1951	249	25
Brixham	August 1952	170	10
Plymouth (Tinside)	August 1950	56	59
Plymouth (Phoenix Wharf)	November 1951	102	28
Looe	September 1949	43	47
Par	January 1950	50	94

frequent breeding of *Elminius* (Crisp & Chipperfield 1948) might enable the latter to survive. However, this explanation can at the best be but a partial one, for the decline in *Balanus* has occurred over a much wider area than the increased infection by *Hemioniscus*. It seems more likely that the great incidence of *Hemioniscus* in the south and west is a further indication of the poor condition of the *Balanus* in those areas (Fig. 5).

(*b*) *Physical*

So far as we are aware, only two factors have been considered seriously as influencing the distribution of *Chthamalus stellatus*, the favourable effect of Atlantic Water (Moore & Kitching 1939) and the unfavourable effect of low temperature (Southward 1950, Kitching 1950). These factors are not readily distinguishable, as climatic conditions are themselves so dependent upon the proximity of the major water masses. Neverthe-

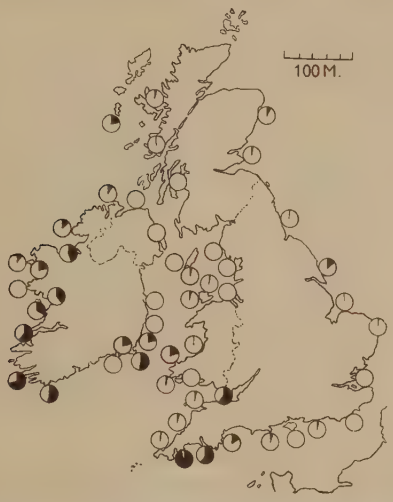

Fig. 5. The relative proportions of specimens infected with *Hemioniscus balani* (black) in the populations of *Balanus balanoides* at places round the British Isles, 1949–52.

less, the present geographical distribution seems better explained in terms of temperature, for the main boundary of *Chthamalus* approximates to the February air isotherm for 5° C., while the main southern boundary of *Balanus balanoides* runs approximately between the winter sea-water isotherms for 8 and 9° C.

It has been shown (Crisp 1950) that adult *Chthamalus* can survive without great mortality for at least two winters on the coldest parts of the east coast (Whitley Bay and North Norfolk) and that they can produce apparently normal nauplius larvae during the succeeding summer. It is not, however, known whether these nauplii would be able to complete their planktonic development. These observations suggest that the limitation of the environment operates on larval stages rather than on the adult, but against this must be reckoned the fact that the planktonic larvae of *Chthamalus* are present and settle only in the warmest months, whereas the correlation of distribution appears to be with the winter isotherms. Moreover, unpublished experiments in which adult barnacles were subjected to low temperatures indicate that *Chthamalus* is more profoundly affected than *Balanus balanoides*, but the treatment required to demonstrate this is severe and such that the species will hardly ever encounter on the British coast.

In the Brixham area, the breeding of *Balanus* has been studied since 1946. Between 1948 and 1951, the period of the decline in *Balanus*, fertilization of the eggs in November and liberation of the nauplii in February to March appeared to proceed quite normally. Early larvae were present in the plankton but cypris larvae were not very common, and the settlement of spat in these years showed a marked fall. Owing to the discriminating behaviour of barnacle larvae on spatfall (Knight-Jones & Stevenson 1950) it is difficult to measure a representative settlement, but Table 4 gives

Table 4. *Settlement of* Balanus balanoides *at Brixham, 1946–52*

	Date of commencement	End of settlement	Details	Assessment of settlement on open coast
1946	—	—	Heavy settlement observed on 8–9 Apr.	Heavy (very heavy in River Dart)
1947	20 Apr.	—	Fair settlement on water line 24 Apr.	Fairly heavy
1948	8–17 Mar.	Before 5 May	8 spat/cm.^{2} in enclosed waters of harbour	Fair
1949	8 Mar.	25 Apr.	7·5 spat/cm.^{2} on suitable surface at end of settlement	Fair
1950	2 Apr.	20 Apr.	3·6 spat/cm.^{2} on suitable surface at end of settlement	Poor (moderate in estuary of River Dart)
1951	6 Apr.	13 Apr.	Only a very few cyprids observed settling	Very poor
1952	—	—	2·0–2·5 spat/cm.^{2} at M.T.L. on 17 Aug.	Moderate

an approximate comparison. It is obvious that there was a considerable decline in the settlement from 1949 to 1951, and that this was especially marked on the open coast. We can but presume that the larvae failed to mature successfully. Complete failure of the *B. balanoides* settlement in certain years has also been noted in the Plymouth area by Harris (1946).

Thus, in *Balanus*, and possibly in *Chthamalus*, the younger stages seem to be the most vulnerable when the barnacle is growing close to the limits of its distribution. This may be another example of the well-established principle, that while normally many Boreal animals can stand considerable temperature ranges, during the breeding period they become more stenothermic (Apellöf 1912, Orton 1920, Runnström 1929, Ekman 1953). Therefore a general rise in temperature might be expected to favour *Chthamalus* the southern species at the expense of *Balanus* the northern species. The general inverse relationship shown by the species during the recent changes, even in the Isle of Man where direct competition is small since the zones are almost separate, would appear to support this expectation, and certainly suggests the influence of some single factor. Before examining possible correlations between temperature variations and changes in barnacle populations it should be pointed out that some lag is to be expected before the effects of temperature change would normally be shown.

The population of both *Chthamalus* and *Balanus* at high water appears to be made up of age-groups extending over several years, probably 4 or 5 at least, whereas at low water where growth is more rapid survival is reduced and only a small proportion enter the third year of growth. On the whole the longevity of the majority may be put at

about 2–3 years. Breeding commences in *Chthamalus* in the first summer approx. 9–10 months after settlement, and according to Moore (1936) in *Balanus balanoides* either in the first autumn for individuals growing close to low water, or in the second autumn (approx. 20 months after settlement) for individuals higher up the shore. In the Brixham area in favourable situations many individuals at H.W.N. produce fertilized eggs in their first year. Thus a poor settlement in one year will reduce liberation

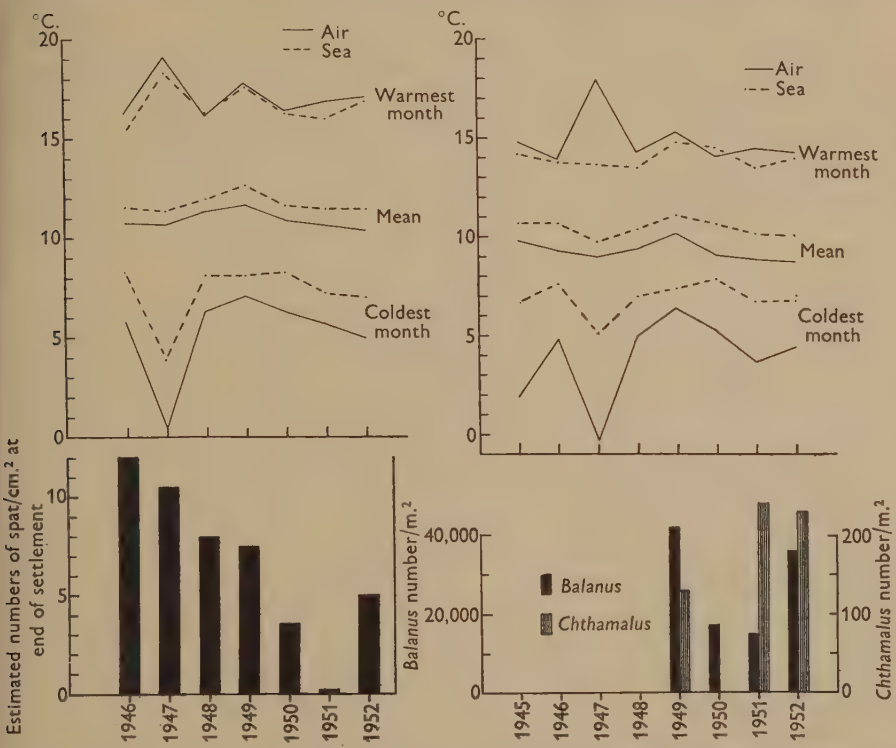

Fig. 6. Left: variation in the density of settlement of *Balanus balanoides* at Brixham, in relation to temperature changes at Torquay. Right: fluctuations in the maximum populations of *Chthamalus stellatus* and *Balanus balanoides* at Kallow Point, Port St Mary, Isle of Man, in relation to some temperature changes.

of larvae in the succeeding year, and this effect may become cumulative, especially if it continues for more than 2 years. Should this occur the survival of the population is dependent upon the few older individuals surviving at high water, or upon specimens in specially favoured situations.

It is fairly well known that temperatures in the neighbourhood of the British Isles were somewhat higher during 1948–51 than in the preceding years; this could be the main cause of the change in the barnacle populations. It is necessary to take into account both sea and air temperatures, as the barnacles are exposed to the influence of both. The left-hand part of Fig. 6 compares the estimated settlement of *B. balanoides*

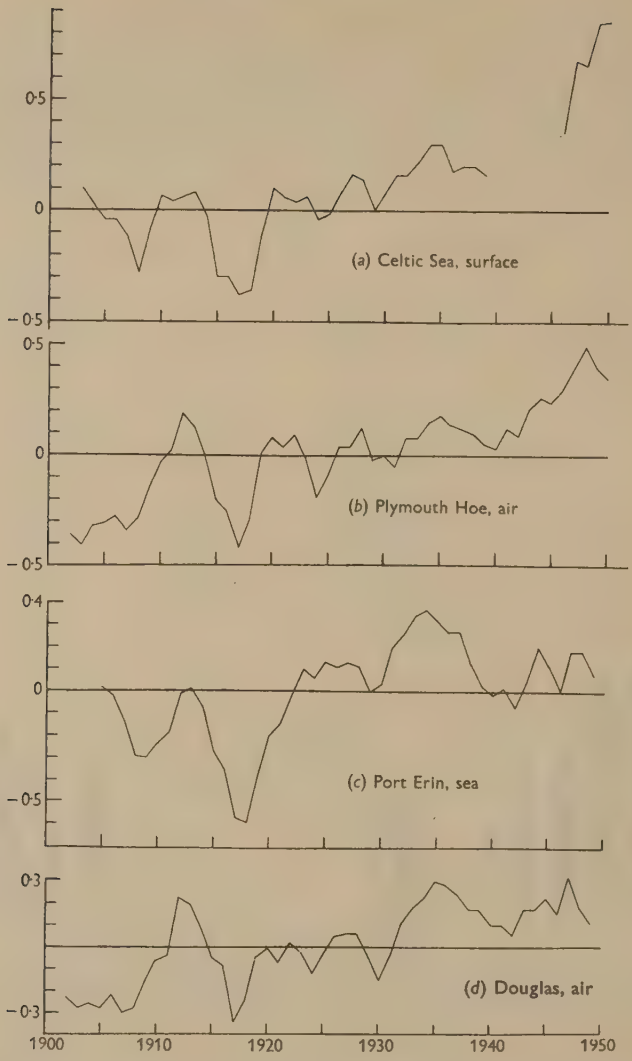

Fig. 7. Five-year running means (anomalies, ° C.) of (*a*) the surface temperature of the Celtic Sea (International Council area P) 1903–39 and 1946–50 (based on Smed 1952); (*b*) air temperature at Plymouth Hoe, 1900–51; (*c*) the surface sea temperature at Port Erin, Isle of Man, 1903–50; (*d*) the air temperature at Douglas, Isle of Man, 1900–50.

(based on Table 4) at Brixham with the variations in sea and air temperatures at Torquay nearby. Allowing for some delay for the effects to be felt, it seems quite possible that the high overall air and sea temperatures in 1948, 1949 and 1950 could have initiated and continued the decline in settlement during 1948–51. It is also possible that the reversal of this trend in 1952 could have resulted from the lower

mean and winter temperatures in 1951 and 1952. The right-hand part of Fig. 6 compares the maximum populations of the two species of barnacle at one part of the area investigated at Port St Mary, Isle of Man (line *D* on Figs. 2 and 3) with variations of air temperature at Douglas and sea temperature at Port Erin. It is again possible that the higher temperatures could have caused the decline in the *Balanus* population and the increase in *Chthamalus* between 1949 and 1951. The partial resurgence of *Balanus* in 1952 could also have been due to the somewhat lower mean temperatures in 1951 and 1952.

In fact, the trends are remarkably similar at both Brixham and Port St Mary, which further strengthens the view that the temperature changes were the causative factors behind the barnacle changes. It must, however, be pointed out that there is no conclusive evidence that this is a direct effect, nor indeed, an obvious one. Higher winter temperatures might, for example, cause abnormalities in the early embryonic life of *Balanus* and render many of the larvae ultimately non-viable. The effect might also operate nutritionally through changes in the phytoplankton succession.

POSSIBLE SECULAR TRENDS

In the absence of other known widespread environmental changes it is likely that the changes in the barnacle populations can be ascribed to a slight but general rise in temperature. This immediately suggests that the recent changes might be part of a long-term trend related to the amelioration of climatic conditions in the northern hemisphere during the past hundred years (Ångstrom 1939, Manley 1946, Ahlmann 1949). Unfortunately the only previous quantitative work dates from so recently as 1932–38, but even so the present distribution of *Balanus* and *Chthamalus* is in many places (Fig. 4) very different from that existing 20 years ago. In the Plymouth area the running means (Fig. 7) show that the general sea and air temperatures during the half-decade ending in 1950 were higher than they had ever been since regular observations began (only the 1900–50 portion of the air temperatures is shown). Almost certainly this will have had some effect on the fauna, and is most probably the cause of the difference in the barnacle population in 1951 compared with 1934. In the Isle of Man, however, the temperatures during the past half-decade appear to have been no higher than those in the 'thirties, and the whole temperature trend is less obvious than that at Plymouth. In this case there is no conclusive evidence that the barnacle population to-day is any different from that in the 'thirties, although there have been recent changes.

Only future investigations can show whether any of the suggestions we have made are correct. If they are, then changes in the barnacle populations may be a guide to changes affecting organisms of economic importance. Environmental effects might be expected to appear in the barnacle populations within a much shorter time than is possible with most organisms of economic importance. Moreover, barnacles are much more readily subject to quantitative survey; they are sessile, and the possibility of temporary migrations can be ruled out.

ACKNOWLEDGEMENTS

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SUMMARY

1. During the past 4 years observations have been made on the distribution of the intertidal barnacles *Chthamalus stellatus* and *Balanus balanoides* around the British Isles.

2. The observations indicate that there has been a change in the relative proportions of these species, *Balanus* having apparently retreated from its southern and western limits while *Chthamalus* has advanced. This change appears to have been most marked in the south-west of England, where a large part of it seems to have taken place between 1949 and 1951.

3. Of various possible causes of this change, the recent encroachment of the immigrant barnacle *Elminius modestus*, and the present high rate of infection of *Balanus* by *Hemioniscus balani*, can be ruled out as major factors, since the change is more widespread than the distribution of *Elminius* or the area of high *Hemioniscus* infection.

4. Examination of temperature records suggests that the high air and sea temperatures occurring in the period 1948–51 might have been responsible for the decline in *Balanus* and increase in *Chthamalus*. The effect seems to have operated on the younger stages but whether it was direct or not is unknown.

5. It is possible that the recent changes may be part of a long-term trend related to the amelioration of climatic conditions in the northern hemisphere during the past hundred years, but further observations are desirable.

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Smed, J. (1952). Monthly anomalies of the surface temperature in the Celtic Sea during the years 1903–39 and 1946–50. *Ann. biol. Copenhague*, **8**, 58–62.

Southward, A. J. (1950). Occurrence of *Chthamalus stellatus* in the Isle of Man. *Nature, Lond.* **165**, 408–9.

Southward, A. J. (1951). Distribution of *Chthamalus stellatus* in the Irish Sea. *Nature, Lond.* **167**, 410–11.

Southward, A. J. & Crisp, D. J. (1952). Changes in the distribution of the intertidal barnacles in relation to the environment. *Nature, Lond.* **170**, 416–17.

Williams, G. (1950). Distribution of *Chthamalus stellatus* on the shores of north-east Ireland. *Nature, Lond.* **166**, 311.

REVIEWS

ZOOLOGICAL TAXONOMY

E. Mayr, E. G. Linsley and R. L. Usinger (1953). *Methods and Principles of Systematic Zoology*. Pp. x + 328; 45 text-figures. New York, Toronto and London: McGraw-Hill. Price 51*s*. ($6.00).

The authors have set out, it would seem, to write a book for someone freshly graduated and about to start taxonomic work at a remote university with no other taxonomist. They have done it well. The style is clear, the triple authorship does not obtrude, pet hobby-horses are kept securely stabled, and there is evidence of a wide knowledge of the subject. The only criticism that may be levelled is that the authors embark on one or two topics, illustrating papers is one that comes to mind, for the adequate exposition of which they have not space, and they would have done better to content themselves with a reference.

The book is in three parts. In the first there is a discussion of the history and purpose of taxonomy and an excellent account of modern ideas about what a species is. In Part 2 there is a good deal of information about purely technical matters such as making a key, preparing a paper for publication and correcting a proof; and the sort of characters on which species and other categories may be separated. One chapter is about quantitative methods and statistics.

In Part 3 there is an account of the history of nomenclature, chiefly since the formulation of the International Code. Then, under the headings: the principle of priority, the type method, specific and intraspecific names, and higher categories, the purposes and application of the rules are discussed. The rules themselves and the opinions are not reproduced.

Part 1 should have a wide appeal for zoologists, particularly those who teach. Parts 2 and 3 are more for the taxonomist. The worker with experience will skip some of the purely technical chapters, particularly in Part 2, but will find the ideas in the others stimulating, even when he does not agree with them, and will appreciate having so much information gathered together in one volume. But what is a taxonomist? The conventional picture of the museum worker framed in store-boxes or glass-bottles is becoming out of date. The authors distinguish three steps: alpha taxonomy is the naming and distinguishing of species, beta taxonomy the arranging of them in a natural system of higher and lower categories. All this may take place within the four walls of a museum, but when the gamma stage is reached, and the status of a single species comes under investigation, taxonomy, ecology, physiology, and genetics become inextricably mixed. Many groups of animals are near or at the gamma stage, so this is a timely book which should be widely read.

T. T. MACAN

ANIMAL SOCIOLOGY

O. W. Richards (1953). *The Social Insects*. Pp. 219; 51 photographs; 12 text-figures. London: McDonald. Price 15*s*.

There has always been a particularly wide interest in the social insects not only amongst professional and amateur entomologists, but amongst the lay public, because of the fascinating problems of social organization and behaviour, and of caste differentiation which they at once raise in our minds. Nowadays the literature on them is so vast and so specialized that no one could hope to cover more than a small proportion of all that has been written. This book is very welcome because it provides a sound and very readable summary of our present-day knowledge.

Dr Richards has long been interested in the social insects and has studied them not only in this country, but in the tropics, so he is able to take a well-balanced view of the many problems they present.

When William Morton Wheeler's fascinating book with the same title was published 25 years ago, it was written for the technical entomologist. Dr Richards's book will commend itself not only to the specialist, for it is accurate and up-to-date, but also to the general ecologist and the layman because of its lucid use of simple English, and it will be found stimulating by all readers because of the author's readiness to distinguish between what is known and generally accepted, what is obscure, and what remains mysterious and unexplained.

The book is divided into nine chapters, the first of which, 'the insect world' serves as an introduction, but rapidly leads to a discussion of the basic behaviour of insects and of social insects in particular. In this, as in the other chapters, only an elementary knowledge of entomology is assumed, and common names are used wherever possible for the insects used as examples. In the second and third chapters, on solitary and social wasps he shows how the life of the solitary forms intergrades with that of the simpler social species, and with the aid of some very good photographs gives a clear idea of the life of the common European wasps *Polistes* and *Vespula*.

Chapters 4 and 5 deal with bees, and the discussion leads up to a useful summary of the new-found knowledge of the honeybees' ability to indicate to other foragers the direction, distance and nature of a source of food.

The next three chapters are on ants, social parasites, and on termites, and it is particularly in the chapter on termites that the change in viewpoint in the last 25 years is shown. In Wheeler's time the causes of caste differentiation were not at all understood, and the apparently conflicting observations left opposing theorists with a very free hand. The comprehensive laboratory experiments conducted particularly in Europe and California have entirely changed and enriched our ideas of these fascinating insects.

In his final chapter on insect societies the various threads from previous chapters are brought together, and the ways in which the societies of ants, bees, wasps, termites and men differ from each other are discussed.

The book is well illustrated, the half-tone blocks being specially good, with the exception of that of the drone, queen and worker of the honeybee. There is an index and a short list of books for further reading. Original sources of information can usually be located by the more serious students because authors' names are quoted. The omission of detailed references cannot be regarded as a serious defect in a book which is primarily written for the non-specialist. The writer is to be congratulated on producing a book which presents the scientific approach to these insects in such a readable form. It should appeal to a wide public. G. C. VARLEY

C. R. Ribbands (1953). *The Behaviour and Social Life of Honeybees.* Pp. 352; 9 plates; 66 text-figures. London: Bee Research Association Ltd. Price 21*s*.

This is an outstanding and scholarly book, which animal ecologists will read with the greatest interest. As soon as the ecology of any animal is investigated, problems of behaviour arise which require solution. In its behaviour the honeybee is a more complex animal than most, and it is fascinating to read of the innumerable experiments which have been performed with these obliging insects. The honeybee has, of course, been domesticated for ages, but recent advances in artificial nest design have had a big effect on our knowledge of its behaviour. (So, too, has the employment of artificial nest boxes for the study of wild birds made certain kinds of field work far easier.)

The method of presentation throughout the book is excellent. Observations and experiments are lucidly described with the help of tables and clear diagrams and simple conclusions are drawn. Those issues (such as the cause of swarming) which are still in doubt are discussed fairly, the evidence is given for both views, and the author then expresses an opinion. The book is divided into four main sections, of which the first, 'the roots of behaviour', is intended for reference, and introduces the reader to the basic facts and theories of vision, taste, smell, hearing, touch and also gives a summary of caste differences, and of the various complex glands which secrete saliva, bee milk, wax and so on.

According to the introduction 'the book proper, which is more readable, commences on p. 69', and the author also rightly claims that scientific jargon is relegated to the foot-notes. However, just occasionally the apiarist's jargon creeps in; some ecologists may puzzle over a 'queenright nucleus'. The three main sections of the book are entitled 'Individual behaviour in the field', 'Communication between honeybees' and 'Life within the community', and each section is split up into short chapters (there are 38 in all). There is a 20-page bibliography, good subject and author indexes, and the half-tone reproductions of photographs of bees are outstanding. The diagrams, graphs, and tables are all carefully provided with explanatory legends, and it is clear that everything has been done to make this a convenient work of reference for the student of animal behaviour, for the ecologist, and of course for the apiarist.

The foraging behaviour of the honeybee provides many problems, and the constancy with

which individual bees collect pollen or nectar from a single species of plant, and the way in which they get new recruits to the prolific crops, are discussed in detail. There are possibilities of persuading bees to concentrate on work of agricultural importance. The influence of food supply on brood rearing shows that under normal conditions the bee is limited by food supply. This book does not consider in detail the problems of bee diseases, bee parasites, and scourges like wax moth, which under wild conditions would have a big influence on survival; but these are of lesser importance under careful domestication.

The last chapter of the book interprets the evolution of the honeybee community in terms of a series of adaptive responses to food supplies. Food is shared between adults. It is passed to the larvae, but those given limited amounts become workers. In the later stages of evolution the feeding of the queen promotes egg production, food transmission enables the workers to forage as a community, to recognize each other, and so defend the colony. The storage of food, and the propagation of the colony by swarming are the final stages in the evolutionary series.

Mr Ribbands is to be congratulated on producing a book which is both authoritative and readable—it deserves every success. G. C. VARLEY

N. Tinbergen (1953). *Social Behaviour in Animals—with Special Reference to Vertebrates.* Pp. xi+150; 8 plates; 67 text-figures. London: Methuen. Price 12*s.* 6*d.*

The publisher describes this book on the dust cover as 'a treatise on the biological study of animal communities'. Treatise seems a grandiloquent word for a book of this size, but it is an admirably clear and concise account, supported by just enough facts, of the point of view and method of approach to the problems of social behaviour, which was initiated by Lorenz and has been developed so rapidly in recent years by his followers including Dr Tinbergen himself. Since it is concerned mainly with the relations between the individual and other individuals of the same species, the word 'community' is used here as the sociologist rather than as the ecologist uses it. Nevertheless, there is much in the book which should be taken into account by anyone working on the autecology of a species. It should, however, be remembered that the method deals especially with those parts of animal's behaviour which are somewhat rigidly automatic, and that there may be other phases of its activity equally important ecologically, which are less amenable to study on these lines. The book is a worthy member of the publisher's well-known series of monographs on biological subjects. H. C. GILSON

THE BRITISH CLIMATE

Gordon Manley (1952). *Climate and the British Scene.* Pp. xviii+314; 32 colour-plates and 41 photographs; 75 text-figures. New Naturalist Series. London: Collins. Price 25*s.*

In his preface the author describes the object of the book as '...to try and bring together the results of qualitative apprehension and quantitative recording, and to provide for those who wish to study any aspect of the natural history of these islands an introduction to its climatology, laying stress wherever one can upon the myriad ways in which the British scene in all its diversity is affected by the vicissitudes, regular and irregular, past and present, of our atmospheric environment.' He goes on to emphasize that 'This is not a meteorological text', but since he also does not assume any but an empirical knowledge of meteorology in his readers, he spends two chapters (after a preliminary one on the history of meteorological recording) in giving a short account of the fundamentals of the meteorology of Britain. The treatment is extremely lucid and the principles are throughout illustrated in terms of familiar weather conditions and actual incidents. If one may be permitted a minor criticism it is that a knowledge of the weather-map symbols is assumed in the reader.

The next three chapters discuss the meteorological conditions and the resulting weather typical of the seasons. This section of the book could, one feels, have been dull, but it is based on such a wealth of knowledge and so freely illustrated, not with vague generalizations but with actual synoptic charts and other meteorological records, that it is in fact quite fascinating.

Then come the four chapters which have perhaps the greatest interest and importance for

ecologists. These deal with the effects of landscape features on weather, with the effects of altitude in relation to mountains and moorlands, and with snowfall and snow-cover. These should be read by everyone engaged in the study of natural populations, whether plant or animal, and will provide much food for thought. This is especially true of the last of the four, in which the author, dealing here with one of his special subjects, stresses the smallness of the quantitative difference between our climate and that of Greenland or northern Scandinavia. In Chapters 12 and 13 the subject-matter becomes more specialized—secular variations of the British climate, and the range of climatic behaviour. In his final chapter the author discusses 'Climate and Man' from a number of points of view. There is here a good deal that is somewhat speculative, but he does not find much difficulty in providing evidence to support his thesis that while its lack of extremes makes it relatively easy to live in, our climate's variability has a beneficial effect on the national character by keeping us alert.

The style throughout the book is clear, straightforward and readable, and the text-figures are adequately described and mostly well-placed in the text. The plates make it a real pleasure to flick over the pages, but they are not merely beautiful but apt as well, and have evidently been chosen with care. Of the colour photographs those by Mr Cecil Newberry stand out as particularly successful. The editors are to be congratulated on having abandoned the photogravure reproduction used in earlier volumes of the series for the excellent half-tones of this one.

H. C. GILSON

ECOLOGY FOR SCHOOLS

Ernest Neal (1953). *Woodland Ecology*. Pp. xii + 107. London: Heinemann. Price 6*s*.

This book is written to introduce the principles of ecology to sixth-form and first-year university students. By limiting its scope to woodland ecology, and in particular to the author's own methods and results in Thurlbear Wood, the book is given a freshness and objectivity which makes it quite outstanding. It avoids all ponderous transatlantic terms, and wisely concentrates on those animals and plants which the ordinary naturalist may be able to identify, and uses common names which embrace many species where possible. The careful avoidance of taxonomic complications makes the book easy to read, but when students come to try in the field the methods advocated, they will at once run into the difficulties of naming their finds. A reference to Smart and Taylor's *Bibliography of Key Works for the Identification of the British Fauna and Flora* (2nd ed., 1953, Systematics Association, British Museum (Nat. Hist.), London) would have been helpful.

The book is divided into fourteen chapters, varying from one to twenty pages in length. After a brief introduction, and a description of the area, its floral composition is considered, and observations of growth period, flowering, pollination and dispersal mechanisms are summarized in simple graphs and tables. Some fifty species of plant, which the student should easily recognize, are listed. The bramble mercifully remains *Rubus fruticosus*; *Carex* is represented only by *C. pendula*; grasses and mosses are scarcely mentioned. Next, habitat factors are considered, and simple methods of measuring light, humidity, etc., and of soil analysis are described, and results given.

The food cycle is concisely dealt with in a couple of pages of text and a simple diagram of the basic food chain. The sixth chapter on the main habitats simply lists those which the author has recognized and studied, and occupies a page! Longer chapters follow on methods of finding animals, on food relationships, and on adaptation to feeding, to reproduction and dispersal, and all are treated with a masterly simplicity. The book ends with a two-page bibliography and a three-page index. It is well illustrated by sixteen clear diagrams, and nine excellent half-tone plates. The author and publishers are to be congratulated on producing a book so free from blemish.

The book does not set out to be a text-book, but is a valuable guide to what beginners in ecology can do for themselves. It gives a good introduction to the inter-relationships between the plants and animals of a wood, and should be very helpful to those who wish to learn, or to teach elementary ecology.

G. C. VARLEY

AFRICAN SIMULIIDAE

P. Freeman and B. De Meillon (1953). *Simuliidae of the Ethiopian Region.* London: British Museum (Nat. Hist.). Price 50*s*.

The present period has seen the publication of a number of valuable reference monographs of groups of biting insects. The present volume is an excellent example of the type. Of the two authors one works in Britain in the British Museum and the other in South Africa in the Institute for Medical Research, a very satisfactory arrangement, for the specimens and other valuable material are for the most part in either one or other of these institutions.

The introduction deals with such things as the life history and habits, methods of collecting material and such other points of general interest. In considering zoogeography it is pointed out that of all the species of *Simulium* which occur in the Ethiopian region, one only is known to occur outside the region. As the distribution of these insects is determined very largely by the existence of waters of specialized types, *Simulium* does not follow the principles which govern the distribution of other insects in the African continent. It would not form a good illustration of the familiar lines of African zoogeography.

The section relating to medical importance and disease gives a good general account of the toxaemic symptoms which result from bites: also of the transmission of *Onchocerca* and of the entomological aspect of the blinding disease which it causes. The authors might perhaps have called attention to a significant point brought out by D. J. Lewis that *Simulium damnosum* frequent and are known to bite man in areas where onchocerciasis does not occur. This may be due only to the fact that the worm has not yet been introduced; but as the absence of the organism seems to be from places where the atmospheric humidity is very low, the phenomenon may probably be due to the fly not generally living long enough for the parasite to complete its cycle. For the event to occur and the transmission of the *Onchocerca* to take place, it would seem that a high degree of atmospheric humidity at least at one season of the year is necessary.

The authors' discussion of the systematics of African *Simulium* is very interesting and should be studied by workers on these insects in other parts of the world. The females, which are much easier to catch, may be extremely difficult or impossible to identify, so that most of the points of difference between species lie in the male genitalia or in the respiratory filaments of the pupae. These pupal structures may be extremely diverse within a species. In such cases the present authors take a unitarian view refusing at least for the moment to recognize species distinguishable only by characters in the pupae. Accepting that rather conservative view of the matter they find that there are at present known from the Ethiopian region of Africa, sixty-three species of *Simulium* and six species of the related genus *Cnephia*.

The more specialized part of the book gives keys to species, technical descriptions on points of classification and descriptions of species. The general level of scholarship and of production is, as need hardly be said, very high. P. A. BUXTON

BOOKS RECEIVED

Fundamentals of Ecology. By Eugene P. Odum. Philadelphia and London: W. B. Saunders Co. 1953. Price 32*s*. 6*d*.

A Herd of Mule Deer. By Jean M. Linsdale and P. Quentin Tomich. Berkeley: University of California Press (London: Cambridge University Press). 1953. Price 64*s*.

The Fulmar. By James Fisher. London: Collins. 1952. (New Naturalist.) Price 35*s*.

A Thousand Geese. By Peter Scott and James Fisher. London: Collins. 1953. Price 21*s*.

Wildlife in Alaska—an Ecological Reconnaissance. By A. Starker Leopold and F. Fraser Darling. New York: Ronald Press. 1953. Price $2.75.

Tissue Culture. By E. N. Willmer. Second edition, revised. London: Methuen. 1953. Price 9*s*. 6*d*.

The Nuffield Foundation—Eighth Report. 1953. Oxford.

ABSTRACTS

Abstracts are now appearing from the following journals and publications:

Agriculture
Ann. Appl. Biol.
Ann. Mag. Nat. Hist.
Antiquity
Biol. Rev.
Biometrika
Brit. J. Anim. Behaviour
Rep. Brit. Trust Ornith.
Bull. Ent. Res.
J. Conchol.
Rep. Dove Mar. Lab.
Entomologist
Ent. Mon. Mag.
Ent. Rec.
Fish. Invest. Lond.
J. Gen. Microbiol.
J. Hyg., Camb.
Linn. Soc. Lond. Proc. & Trans.
Lond. Nat.
Proc. Malacol. Soc.
J. Mar. Biol. Ass. U.K.
Rep. Mar. Biol. Stn Pt. Erin
Naturalist
Nature, Lond.
New Biol.
Parasitology
Proc. Prehist. Soc.
Quart. J. Micr. Sci.
R. Ent. Soc. Lond. Proc. & Trans.
Roy. Soc. Proc. & Trans.
Roy. Soc. Edinb. Proc. & Trans.
Roy. Hort. Soc. J.
Roy. Irish Acad. Proc.
Salm. Trout Mag.
Sci. News
Scot. Home Dep. Sci. Invest.
Scot. Mar. Biol. Ass. Coll. Reprints
Scot. Nat.
Proc. Zool. Soc. Lond.

and the journals and proceedings of local natural history societies.

The list of publications it is impossible to cover regularly without further assistance includes:

Bird Notes
Rep. Bd. Greenkeeping Res.
Brit. Birds
Countryside
Discovery
Rep. East Malling Res. Stn
Endeavour
Ibis
Rep. Int. Cttee Bird Pres.
Proc. Leeds Phil. Lit. Soc.
Proc. Lpool Biol. Soc.
J. Pomol.
Quart. J. Forestry
Roy. Dublin Soc. Proc. Econ. & Sci.
Rep. Roy. Soc. Protect. Birds
Scot. Agriculture
Scot. Forestry
Welsh J. Agriculture
Wye Coll. J.

The abstracts are edited by Prof. L. A. Harvey with the assistance in selection and abstracting of J. D. Brayshaw, D. H. Chitty, G. I. Crawford, A. E. Ellis, P. D. Gabbutt, Miss U. Grigg, N. A. Holme, A. Macfadyen, C. Matheson, Miss E. Nelmes, G. G. Vickers and M. Williamson. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations can greatly aid this work by making sure that copies of their publications are sent, regularly, to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** It has recently become noticeable that some organizations have sent their material only at irregular intervals. Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Prof. L. A. Harvey, University College, Exeter.** In view of the list of journals above from which it is at present impossible to provide abstracts, the services of several new volunteers will be very welcome.

Separate copies of the abstracts suitable for mounting on cards can be obtained from **The Cambridge University Press, 200 Euston Road, London, N.W. 1,** or through any bookseller; price 5*s.* 6*d.* per annum, post free (issued in May and November). Back numbers of the 'Notices of publications...' from Vol. 3 (1934) to Vol. 20 (1951) may also be had at 2*s.* for each annual set of two parts.

CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *Bird Notes* and *British Birds* which would fall in '4. FOOD AND FOOD HABITS';

(*b*) papers in the above two journals and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION'.

	PAGE
1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS	185
(*a*) Marine and brackish	185
(*b*) Fresh water	186
(*c*) Land	188
2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS	191
3. PARASITES	197
4. FOOD AND FOOD HABITS	199
5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION	202
6. STUDIES ON BEHAVIOUR	208
7. REPORTS OF ORGANIZATIONS	210

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) MARINE AND BRACKISH

Barrett, J. H. (1953). A preliminary list of the fish of Dale Roads. *Rep. W. Wales Fld Soc.* **15**, 32–36.

A brief outline of ecological conditions followed by a list of 62 species with notes on size and local frequency.

Burdon-Jones, C. (1952). Development and biology of the larva of *Saccoglossus horsti* (Enteropneusta). *Philos. Trans.* (B) **236**, 553–589.

Describes a laboratory method of rearing *S. horsti* (from the Solent) and details developmental history from the egg to the 5 gill-slit stage. The planktonic larvae hatch 30–36 hr. after fertilization, and settle some 2 days after hatching. There is no sudden metamorphosis, and the total dispersal period may amount to 7 days. There is some evidence of gregariousness in settling larvae. Methods of swimming, feeding and burrowing in the larvae are described and discussed.

Clark, R. B. (1952). Speciation of Polychaetes in the Clyde sea area. *Nature, Lond.*, **169**, 975.

A list of Polychaetes which show morphological differences from typical forms is provided. As it is probable that the variants have lost their pelagic larval phases, it is possible that small interbreeding populations of each species may have arisen.

Davies, J. L. (1953). Colony size and reproduction in the Grey Seal. *Proc. Zool. Soc. Lond.* **123**, 327–332.

Small breeding colonies with high infant mortality and low reproduction rate are probably augmented from larger colonies.

Gauld, D. T., Bagenal, T. B. & Connell, J. H. (1953). The marine fauna and flora of St. Kilda, 1952. *Scot. Nat.* **65**, 29–49.

An ecological survey, with lists of Porifera, Coelenterata, Annelida, Crustacea, Pycnogonida, Insecta, Mollusca, Bryozoa, Echinodermata, Tunicata and Pisces.

Glynne-Williams, J. & Hobart, J. (1952). Studies on the crevice fauna of a selected shore in Anglesey. *Proc. Zool. Soc. Lond.* **122**, 797–824.

Physical measurements and tidal levels of crevices are related to a fauna of 49 species; these include 'terrestrial' and 'marine' animals. There is strict limitation as to vertical level and terrestrial forms are commoner deep in the crevices. Feeding studies in field and laboratory are used to construct the 'food web' and the presence of two alternating 'food-chains' is stressed.

Jones, J. R. Erichsen (1952). The reactions of fish to water of low oxygen tension. *J. Exp. Biol.* **29**, 403–415.

Experimental results from *Gasterosteus aculeatus*, *Phoxinus phoxinus*, and *Salmo trutta* show that water of low oxygen tension is avoided on account of a very rapid development of respiratory distress followed by random movement; the fish have no immediate appreciation of low oxygen tension.

McCartan, L. & Slinn, D. J. (1953). The effect of a freshwater stream on the ecology of a rocky shore at Carnalea, Co. Down. *Irish Nat. J.* **11**, 70–76.

Observations on the zonation of intertidal animals.

Norris, E. & Crisp, D. J. (1953). The distribution and planktonic stages of the Cirripede *Balanus perforatus* Bruguière. *Proc. Zool. Soc. Lond.* **123**, 393–409.

Seasonal and special distribution in Britain. Descriptions of immature stages.

Southward, A. J. & Crisp, D. J. (1952). Changes in the distribution of the intertidal barnacles in relation to the environment. *Nature, Lond.* **170**, 416–417.

Critical observations show that *Balanus balanoides* is withdrawing from its southern and western limits and this accompanied by a corresponding increase in *Chthamalus stellatus*. A number of factors which may be operative are discussed.

Telfer, I. M. & Watt, G. (1953). The grey seals of the Farne Islands. *Trans. Nat. Hist. Soc. Northumb.* **10**, 165–182.

A preliminary account of work now being carried out on the grey seal (*Halichoerus grypus*) colony at the Farne Islands, the only breeding station on the east coast of Great Britain. Weights and measurements of calves are given, as are the first results of a marking scheme, started at the Farnes, and now being extended to other British colonies.

(*b*) Fresh water

Badcock, R. M. (1952). Observation of egg-laying under water of the aerial insect *Hydropsyche angustipennis* (Curtis) (Trichoptera). *Nature, Lond.* **170**, 40–41.

Fryer, G. (1953). The occurrence of *Gammarus lacustris* G. O. Sars, and *Gammarus pulex* (L.) in Malham Tarn, and a note on their morphological differences. *Naturalist*, **1953**, 155–156.

Examination of a number of Amphipods from Malham Tarn provided the first record of *G. lacustris* for England. The author deals with the occurrence of this species, and of *G. pulex*, and suggests that their ecology might be studied by students visiting the study centre.

Fryer, G. (1953). Notes on certain British freshwater Crustaceans. *Naturalist*, **1953**, 101–109.

Includes notes on dispersal mechanisms in Ostracoda, Crustacean fauna of submerged stones, and *Cyclops viridis* attacking a recently hatched fish (? a roach).

Galliford, A. L. (1953). Notes on the aquatic fauna of the Freshfield-Ainsdale and Hightown sand-dunes. *Proc. Lpool Nat. Fld Cl.* **1953**, 25–27.

Lists of Rotifera and Cladocera, with a description of the habitat.

Gibson, F. A. (1953). Brook lamprey, *Lampetra branchialis* Day, in a Westmeath stream. *Irish Nat. J.* **11**, 86–89.

Notes on length frequency, stages of maturity and egg counts based on a collection of 75 specimens, and on stomach contents based on a collection of ammocoetes larvae.

Hall, R. E. (1953). Observations on the hatching of eggs of *Cheirocephalus diaphanus* Prévost. *Proc. Zool. Soc. Lond.* **123**, 95–109.

The known irregular appearance of this species and its ability to breed continuously under suitable conditions are largely accounted for by observations on the breaking of egg membranes and experiments on the effects of desiccation.

Hanney, P. (1953). An introduction to the Chiltern dew-ponds. *Reading Nat.* **5**, 4–7.

An account of some animals (Amphibia and invertebrates) in two dew-ponds of different ages, with some comparative notes.

Harker, J. E. (1952). A study of the life cycles and growth-rates of four species of mayflies. *Proc. R. Ent. Soc. Lond.* (A) **27**, 77–85.

The species are *Ecdyonurus torrentis*, *Rithrogena semicolorata*, *Heptagenia lateralis* and *Baetis rhodani*.

Holway, P. H. & Cocking, A. W. (1953). Observations on the vertical distribution of *Bosmina* spp. (Crustacea: Cladocera) in Malham Tarn and in Grasmere. *Ann. Mag. Nat. Hist.* (12) **6**, 717–720.

B. obtusirostris mainly in the top 15 cm. of open water in Grasmere, absent from Malham Tarn: *B. longirostris* among weeds in shallow water in Grasmere, probably in the top 15 cm. of open water at Malham. Other Cladocera not stratified, at least in top 30 cm.

Jones, J. W. & King, G. M. (1952). Spawning of the male salmon parr (*Salmo salar* Linn. juv.). *Nature, Lond.* **169**, 882.

Mackay, I. (1952). Observations on the amphipod *Eucrangonyx gracilis* S. I. Smith. *Rep. Oundle Sch. Nat. Hist. Soc.* **1951**, 5–10.

Experiments on the effects of temperature, current and light.

Philipson, G. N. (1953). The larva and pupa of *Hydropsyche instabilis* Curtis (Trichoptera: Hydropsychidae). *Proc. R. Ent. Soc. Lond.* (A) **28**, 17–23.

Includes a few notes on shelter construction and feeding.

Reynoldson, T. B. (1953). Habitat of *Polycelis felina* (= *cornuta*) and *Crenobia alpina* in the British Isles. *Nature, Lond.* **171**, 660.

Both these Triclads are regarded as stenothermous, stream dwelling species, but it is shown that they occur in a number of named Argyll lochs. Several environmental factors are discussed in the light of new experimental work.

Stuart, T. (1953). Water currents through permeable gravels and their significance to spawning Salmonids, etc. *Nature, Lond.* **172**, 407–408.

A model is described which demonstrates the probable relationship between current, gravel composition, and the successful spawning of the minnow, *Phoxinus phoxinus*.

Taylor, M. (1952). *Amoeba hugonis* n.sp.: life-history. *Quart. J. Micr. Sci.* **93**, 427–433.

Material collected from Loch Tannoch, Milngavie was found to contain this new species. The life-history was found to be similar to that of *Amoeba proteus*.

Warwick, T. (1952). Strains in the Mollusc *Potamopyrgus jenkinsi* (Smith). *Nature, Lond.* **169**, 551–552.

Descriptions are given of the more important strains of this Mollusc. Experiments indicate that certain morphological characters are induced by algal metabolites.

Went, A. E. J. (1953). Notes on some Irish char, *Salvelinus* spp. IV. *Irish Nat. J.* **11**, 91–97.

Descriptions of 33 specimens of *S. colii* and two specimens of *S. obtusus*, with some observations on growth rates.

(*c*) Land

Anderson, L. F. (1953). Effect of the war years on the birds of Bucklebury Common. *Trans. Newbury Fld Cl.* **10**, 16–18.

The effect on the birds of a Berkshire common of the establishment of a military camp.

Anon. (1953). Birds in a blizzard. *Middle-Thames Nat.* **5**, 11.

Notes on the effect of the blizzard of 29 March 1952, on 49 nests (mistle-thrush, song-thrush, blackbird, hedge-sparrow), of which only 16 survived.

Barnes, H. F. (1953). The absence of slugs in a garden and an experiment in re-stocking. *Proc. Zool. Soc. Lond.* **123**, 49–58.

Arion reticulatus was introduced to a garden where it had been exterminated by drought. Subsequent history followed through three years.

Beven, G. (1953). Further observations on the bird population of an oakwood in Surrey (Eastern Wood, Bookham Common). *Lond. Nat.* **32** (1952), 51–77.

A detailed account with censuses of robin, blackbird and willow warbler territories, and of blue and great tits. Some measurements of song output.

Braham, A. C., Murgatroyd, J. H., Butler, P. M., Hincks, W. D., Shaw, S. & Steel, W. O. (1953). The entomology of Spurn Peninsula. *Naturalist*, **1953**, 125–140, 157–172.

A further instalment of the paper started in 1951. Separate sections deal with Coleoptera Staphylinidae, Hymenoptera, Diptera, Siphonaptera and Anoplura, Arachnida and other invertebrates and vertebrates, excluding birds.

Broadbent, L. (1953). Aphids and virus diseases in potato crops. *Biol. Rev.* **28**, 350–380.

The study of the factors affecting the spread of viruses. These include time of arrival and frequency of movement of the aphids, climatic and agricultural regime. Among topics discussed are: relation of microclimatic to screen readings, conditions of flight, effects of predators, parasites and insecticides.

Brunt, Sir D. (1953). Bases of micro-climatology. *Nature, Lond.* **171**, 322–323.

Considers the climatology of bare soil and then discusses the effect of vegetation, contour and aspect.

Chitty, D. (1952). Mortality among Voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire, in 1936–39. *Philos. Trans.* (B) **236**, 505–552.

Field vole populations were studied by marking and recapture and showed cyclic fluctuations with a period of about 4 years. High mortality not explicable by epizootic disease is hypothetically explained as due to intraspecific strife which produced physiological effects transmissible to the next two generations.

Crooke, M. (1953). Some notes on *Anoplonyx destructor* Benson. *Bull. Ent. Res.* **44**, 77–81.

Notes on the life-history (parthenogenetic), descriptions of larval instars, distribution in Britain, and economic status of this larch-feeding sawfly.

Cumber, R. A. (1952). Notes on the biology of *Melampsalta cruentata* Fabricius (Hemiptera-Homoptera: Cicadidae), with special reference to the nymphal stages. *Trans. R. Ent. Soc. Lond.* **103**, 219–237.

The life history is studied and there is a description of the nymphal stages. Included is a list of parasites and commensals.

Davies, M. E. & Edney, E. B. (1953). The evaporation of water from spiders. *J. Exp. Biol.* **29**, 571–582.

Four species were used for experiments on water retention. The trachaeae are unimportant, evaporation from lung-books depends greatly on whether they are open, evaporation from the integument is similar to that from insects and the effects of temperature and abrasive dusts indicate that a wax layer is present in the cuticle.

Edney, E. B. (1952). Body temperature of Arthropods. *Nature, Lond.* **170**, 586–587.

Field experiments with *Ligia oceanica* suggest that, even in direct sunlight, evaporation and convection lower the body temperature.

Edney, E. B. (1953). The temperature of woodlice in the sun. *J. Exp. Biol.* **30**, 331–349.

Experiments on four species of woodlice and the cockroach, in which microclimates and the temperature of the animals were measured, showed that the woodlice remained cooler than the ground. The extent of this effect in the different species corresponds with their ability to evaporate water, except for *Armadillidium*. These results are related to the biology and behaviour of the animals. Evaporation is more important in cooling woodlice than insects.

Freeman, J. A. (1952). Occurrence of Collembola in the air. *Proc. R. Ent. Soc. Lond.* (A) **27**, 28.

Lists a number of species collected from various air traps.

Gardiner, P. (1953). The morphology and biology of *Ernobius mollis* L. (Coleoptera: Anobiidae). *Trans. R. Ent. Soc. Lond.* **104**, 1–24.

An account of the distribution and life history, together with notes on the habits of all stages with special reference to the moulting and growth of the larva.

Gaul, A. T. (1952). The awakening and diurnal flight activities of vespine wasps. *Proc. R. Ent. Soc. Lond.* (A) **27**, 33–38.

Observations on colonies of *Vespula maculifrons*, *Dolichovespula maculata* and *Polistes fuscatus* suggest that these wasps are awakened in the morning when temperature and light reach threshold values. These thresholds, which are specific, may influence the early activities of the queens in the spring and hence may be factors in controlling wasp abundance.

Hampton, U. M. (1952). Reproduction in the house-fly (*Musca domestica L.*). *Proc. R. Ent. Soc. Lond.* (A) **27**, 29–32.

In experiments on the stimulation of females by males, it was shown that virgin flies lay fewer batches, fewer eggs, have longer pre-oviposition periods, and lay less frequently than fertilized flies.

Henderson, M. (1953). Some observations on the rook population of west Cheshire. *Proc. Lpool Nat. Fld Cl.* **1952**, 14–15.

A summary of annual counts during 1944–52, with notes on factors affecting the decrease.

Howe, R. W. & Burges, H. D. (1953). Studies on Beetles of the Family *Ptinidae*. IX—A laboratory study of the biology of *Ptinus tectus* Boield. *Bull. Ent. Res.* **44**, 461–516.

Details studies of life history and range of foods. Two inherited variations are noted. The recorded geographical distribution is compared with the possible range of the species (estimated from laboratory data).

Humphreys, H. (1951). Dental evidence in archaeology. *Antiquity*, 16–18.

The peculiarly durable nature of teeth has made possible for example the preparation of a chart showing the distribution of mammals during the ice ages of the Pleistocene and the inter-glacial epochs. Human teeth owing to their individuality provide a good method of counting heads; they also indicate the variation in the amount of dental caries from one period to another and thus afford at any rate some suggestion as to the type of food consumed.

Johnson, C. G. (1952). A new approach to the problems of the spread of aphids and to insect trapping. *Nature, Lond.* **170**, 147–148.

Current views and recent work on Aphid migration are examined and emphasis is laid on the fact that aerial traps, when used by themselves, are not always suitable for the analysis of population and activity factors.

London Natural History Society (1953). The survey of Bookham Common. Eleventh year. *Lond. Nat.* **32** (1952), 45–77.

An introductory progress report includes brief notes by C. J. F. Bensley on molluscs in ponds formed in gun pits and bomb craters and records by A. E. Le Gros of Hymenopterous parasites reared from spider eggs. M. Niblett reports on the distribution of some 27 Trypetids, believed to be near the total number present, collected as larvae in a systematic search of the food plants, and indicates the food plants and seasonal history of each. G. Beven gives a detailed account, with many graphs and histograms, of further work on the bird population of an oakwood.

Nash, T. A. M. & Page, W. A. (1953). The ecology of *Glossina palpalis* in Northern Nigeria. *Trans. R. Ent. Soc. Lond.* **104**, 71–169.

The method of marking flies is used extensively to give a considerable amount of information on seasonal fluctuations, distribution, concentration, dispersal, fly density, sex ratio, fly breeding and longevity. Climatic, vegetational, and food factors are also dealt with in detail.

Owen, D. F. (1953). The habitats of *Pararge aegeria* L. in southern England. *Ent. Rec.* **65**, 129–130.

In Cornwall, Devon, Somerset and possibly other western counties, this butterfly commonly flies in non-wooded areas and has apparently done so for years. Many records of its occurrence away from woods in eastern districts may be connected with the current eastern extension of its range.

Owen, D. F. (1953). Ecology and distribution of the Satyridae in West Kent. *Lond. Nat.* **32**, 1952, 13–44.

The distribution, habitats and micro-habitats of the eight species that occur in West Kent are described and subjected to a detailed examination in the light of the concept of ecological isolation, which, the author concludes, appears to be applicable to certain of them. Observations on the production of extra broods and the presence of butterflies in lucerne and clover fields under favourable weather conditions are appended.

Perttunen, V. (1952). Seasonal change in the humidity reaction of the common earwig *Forficula auricularia*. *Nature, Lond.* **170**, 209–210.

This earwig shows a preference for low humidities in the summer and higher humidities in the winter. The results are in accordance with observations on the ecology of the species.

Sankey, J. H. P. (1952). The winter macrofauna of an old pine stump on heathland. *Ent. Mon. Mag.* **88**, 223–224.

The author suggests that insects characteristic of heathland, which are distributed over the area in summer, become concentrated into small areas suitable for hibernation in winter, and, in support of this theory, lists the species (newts, molluscs, insects, Polydesmids, Chilopods and Isopods) found in an old pine stump in Surrey.

Spencer, K. G. (1953). Observations on song-thrushes. *Naturalist*, **1953**, 153–154.

Several birds were singing from established song-posts in January 1948. Frost on 25 and 26 February, silenced all except one. A communal roost was used, though some individuals had to fly over several territories to get to it. About the end of February numbers increased from six to twenty or more. Pair formation took place between 14 and 19 March. In mid-April there were eleven territories in the twenty acres. Several instances of aggressive display were seen. The observations were made at Burnley, Lancashire, in an area comprising a park and private gardens adjoining.

Spittle, R. J. (1952). The Coleopterous fauna of grey squirrels' dreys. *Ent. Mon. Mag.* **88**, 163–164.

Includes lists of 35 species taken in 10 dreys in Buckinghamshire and Berkshire, with descriptions of the dreys and details of their situation. A separate list is given of 10 species found in two of the dreys that were built on birds' nests.

Syms, D. (1953). Some notes on the hedgehog (*Erinaceus europaeus* L.). *Rep. W. Wales Fld Soc.* **15**, 24–28.

An account of the mammal's life history, including hibernation, food, and parasites.

Temperley, G. W. (1953). The past and present status of squirrels in Northumberland and Durham. *Trans. Nat. Hist. Soc. Northumb.* **10**, 153–164.

The grey squirrel has not yet penetrated Northumberland where the red squirrel is locally fairly common. In Durham the grey is making little progress but the red is now very rare except in the south-west. The red squirrel population of both counties has been considerably reduced in the last fifty years.

Vernon, E. T. (1953). Notes on the diurnal movements of swifts in Glasgow. *Glasgow & W. Scot. Bird Bull.* **2**, 6–7.

Based on observations that are evidently interesting but of which not enough is said to enable their value to be judged.

Vernon, R. M. (1953). Some observations and breeding records of the lapwing, Skokholm, 1952. *Rep. Skokholm Bird Obs.* **1952**, 25–30.

Mainly on breeding biology, but some notes on predators.

Vine, A. E. (1953). Heronries of the Cambridge district, II. *Rep. Camb. Orn. (Bird) Cl.* **1952**, 21–23.

A summary of the vital statistics of *Ardea cinerea* in Cambridgeshire and the area within eight miles of the county boundary since 1931, when a previous report was published.

Williamson, K. (1953). Report on the arctic skuas, 1953. *Fair Isle Bird Obs. Bull.* **12**, 3–12.

Observations on the breeding biology of 31 pairs of *Stercorarius parasiticus*, including the proportions of pale phase birds.

Williams, T. S. (1953). Observations on sheld-duck on the Welsh side of the Dee estuary. *Proc. Lpool Nat. Fld Cl.* **1953**, 15–18.

Summary of monthly counts of *Tadorna tadorna* on the Flintshire coast during 1950–52, mainly, it is thought, non-breeders.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Bailey, N. T. J. (1953). The total size of a general stochastic epidemic. *Biometrika*, **40** 177–185.

With a constant ratio of infection rate of susceptibles to removal rate of infectious cases. No threshold phenomenon is found. Wide variations in the size of an epidemic can occur by chance with the same infection and removal rates. Graphs are given as well as equations. The distribution of multiple cases in a household is considered. The model does not fit diseases with short periods of high infectivity.

Banks, C. J. (1952). An analysis of captures of Hemerobiidae and Chrysopidae in suction traps at Rothamsted, July, 1949. *Proc. R. Ent. Soc. Lond.* (A) **27**, 45–53.

Describes in detail the method used and the conditions under which trapping occurred. All the Neuropterans were caught at night with the maximum activity (for the Hemerobiidae) during the dusk period. There is, with certain reservations, a positive correlation between 'catch size' and temperature.

Bodenheimer, F. S. (1953). On animal and human populations. *Sci. News, Harmondsworth*, **30**, 43–60.

Reviews some of the classical and more recent studies on population growth and its control, and supports the thesis that future studies of human populations must be incomplete without direct contributions from the animal population ecologist.

Boratynski, K. L. (1952). *Matsucoccus pini* (Green, 1925) (Homoptera, Coccoidea: Margarodidae): bionomics and external anatomy with reference to the variability of some taxonomic characters. *Trans. R. Ent. Soc. Lond.* **103**, 285–326.

The life-history is studied. The species is parthenogenetic and it is shown that there are morphological differences between the two generations produced per year. It is confined to *Pinus sylvestris* and the habits of each of the stages are described.

Cameron, E. (1953). Some new and improved methods for demonstrating the cockroach. *Proc. R. Ent. Soc. Lond.* (A), **28**, 41–44.

Includes a short note on rearing *Periplaneta americana* in the laboratory.

Carvalho, J. C. M. & Leston, D. (1952). The classification of the British Miridae (Hem.), with keys to the genera. *Ent. Mon. Mag.* **88**, 231–250.

Includes keys to the subfamilies, tribes and genera.

Clark, R. B. (1952). New records of sub-littoral polychaetes from the Clyde Sea Area, with a description of a new species. *Proc. Roy. Soc. Edinb.* (B), **65**, 1–26.

Fifty species new to the Clyde Sea Area are recorded, of which nine are new records for British waters. *Amage scotica* n.sp. is described and figured.

Cleat, N. D. (1952). Growth in the laboratory of economically important Oribatid mites. *Nature, Lond.*, **169**, 280–281.

A technique is described for rearing these mites in the laboratory. There are short notes on its life-shitory, and the duration of the stages at constant temperature and humidity.

Collin, J. E. (1953). On the British species of *Scaptomyza* Hardy and *Parascaptomyza* Duda (Dipt., Drosophilidae). *Entomologist*, **86**, 148–151.

Includes a key to the British species of *Scaptomyza*, one of which is described as new.

Collin, J. E. (1952). On the European species of the genus *Odinia* R.-D. (Diptera-Odiniidae). *Proc. R. Ent. Soc. Lond.* (B) **21**, 110–116.

Includes a key for the identification of the four British species.

Craig, C. C. (1953). On the utilization of marked specimens in estimating populations of flying insects. *Biometrika*, **40**, 170–176.

The case in which the individual is released immediately after capture and when the population size is fixed. The total population is estimated from the distribution of the number of individuals marked 1, 2, ..., times. Five methods are given, three of them with variances. Examples are given.

Craig, C. C. (1953). On a method of estimating biological populations in the field. *Biometrika*, **40**, 216–218.

Likelihood estimate of the total population of a well defined region and its variance from the population of a sub-region or from the distribution of distances between nearest neighbours.

Downes, J. A. & Kettle, D. S. (1952). Descriptions of three species of *Culicoides* Latreille (Diptera: Ceratopogonidae) new to science, together with notes on, and a revised key to the British species of the *pulicaris* and *obsoletus* groups. *Proc. R. Ent. Soc. Lond.* (B) **21**, 61–78.

Edney, E. B. (1953). The woodlice of Great Britain and Ireland. A concise systematic monograph. *Proc. Linn. Soc. Lond.* **164**, 49–98.

Keys to species, descriptions, summary of distribution, drawings of parts of most species. Thirty-seven species recorded.

Edney, E. B. (1953). The construction and calibration of an electrical hygrometer suitable for microclimatic measurements. *Bull. Ent. Res.* **44**, 333–342.

An electrolytic hygrometer which may be carried in a suitcase for field use. There is no continuous evaporation of water. Calibration is stable for at least a fortnight and the hygrometer equilibrates within 10 min. Readings may be made from a distance to $\pm 2\%$ from 50% to 90% R.H.; a second element is required for humidities from 10 to 60% R.H. Elements must be re-calibrated if exposed to saturated air and must be calibrated individually.

Evans, D. A. (1953). Experimental evidence concerning contagious distributions in ecology. *Biometrika*, **40**, 186–211.

A study of published data on plants and insects. Neyman Type A, Pólya-Aeppli and negative binomial distributions are fitted. The insect counts were best fitted by the last, which is the most skew. Two methods of fitting each curve and tests for goodness of fit more sensitive than χ-squared are described and illustrated.

Fennah, R. G. (1952). On the classification of the Tettigometridae (Homoptera: Fulgoroidea). *Trans. R. Ent. Soc. Lond.* **103**, 239–255.

A key to the subfamilies of the Tettigometridae is provided.

Fisher, R. (1953). Population genetics. *Proc. Roy. Soc.* (B) **141**, 510–523.

In outlining the place and scope of population genetics, reviews and evaluates various published studies, including well known field studies involving population analysis in Lepidoptera, tsetse-flies, and grouse locusts.

Gnanamuthu, C. P. (1952). A simple device for measuring the volume of an aquatic animal. *Nature, Lond.* **170**, 587.

A volumometer is figured and described.

Haldane, J. B. S. (1953). Animal populations and their regulation. *New Biol.* **15**, 9–24.

An introduction to some aspects of the subject, aiming to stimulate thought and study.

Hall, D. W. & Howe, R. W. (1953). A revised key to the larvae of Ptinidae associated with stored products. *Bull. Ent. Res.* **44**, 85–96.

Keys to the larvae of 15 species of these beetles found in stored products.

Hickin, N. E. (1952). Larvae of the British Trichoptera.—33. *Proc. R. Ent. Soc. Lond.* (A) **27**, 86–88.

The larva of *Polycentropus flavomaculatus* (Polycentropidae) is described and figured.

Hickin, N. E. (1952). Larvae of the British Trichoptera.—34. *Proc. R. Ent. Soc. Lond.* (A) **27**, 89–90.

The larva of *Tinodes assimilis* (Psychomyidae) is described and figured.

Hickin, N. E. (1953). Larvae of the British Trichoptera.—35. *Proc. R. Ent. Soc. Lond.* (A) **28**, 36–38.

The larva and the adult of *Tinodes unicolor* (Psychomyidae) are described and figured. Includes notes on tunnel formation.

Hickin, N. E. (1953). Larvae of the British Trichoptera.—36. *Proc. R. Ent. Soc. Lond.* (A) **28**, 39–40.

The larva of *Phryganea varia* Fabricius (Phryganeidae) is figured and described.

Hickin, N. E. (1953). Larvae of the British Trichoptera.—37. *Proc. R. Ent. Soc. Lond.* (A) **28**, 74–76.

The larva and the adult of *Setodes tineiformis* Curtis (Leptoceridae) are described and figured.

Hickin, N. E. (1953). Larvae of the British Trichoptera.—38. *Proc. R. Ent. Soc. Lond.* (A) **28**, 111–113.

The larva of *Athripsodes bilineatus* L. is described and figured. Includes a figure of the adult.

Hickin, N. E. (1953). Larvae of the British Trichoptera.—39. *Proc. R. Ent. Soc. Lond.* (A) **28**, 114–116.

The larva of *Mystacides longicornis* is described and figured. The adult is figured. Includes a key for the identification of the larvae of the genus *Mystacides*.

Hincks, W. D. (1952). The genera of the Cassidinae (Coleoptera: Chrysomelidae). *Trans. R. Ent. Soc. Lond.* **103**, 327–358.

A key and an index to the tribes of the Cassidinae is given.

Hope, J. A. (1953). A simple method for sexing the confused Flour Beetle. *Nature, Lond.* **171**, 265–266.

Kitchen, W. H. & Gall, D. (1953). A controlled humidifier for insect breeding rooms. *Bull. Ent. Res.* **44**, 367–369.

A method and simple apparatus are described for using an atomizer as a humidifier, for a room about 20 ft. square or more, with a controlling hygrostat. The apparatus may be of especial use where external conditions of high temperature and low humidity prevail, and where high humidities and temperatures are required in the breeding rooms.

Laws, R. M. (1952). A new method of age determination for mammals. *Nature, Lond.* **169**, 972–973.

Depends upon the cyclical variation in the rate and manner of calcification of the teeth. There is a positive correlation between body length and the supposedly annual growth zones in the elephant seal, *Mirounga leonina*.

Leslie, P. H., Chitty, D. & Chitty, H. (1953). The estimation of population parameters from data obtained by means of the capture-recapture method. III. An example of the practical application of the method. *Biometrika*, **40**, 137–169.

A study of two species of vole, *Microtus agrestis* and *Clethrionomys glareolus*. Marked *Microtus* are captured more easily than unmarked, so only the parameters for the marked population can be calculated. No differences were found between the marked animals. The accuracy of these parameters was good. A rough estimate of the total population was got by using the life table of the marked population. There was no apparent distinction between marked and unmarked *Clethrionomys*, so parameters for the total population are calculated. Methods for coping with the absence of certain recapture classes and with the death of animals in traps are described, as are methods for estimating the variances and covariances of the parameters.

Mack, C. (1953). The effect of overlapping in bacterial counts of incubated colonies. *Biometrika*, **40**, 220–222.

Formulae, with standard deviations, for estimating the numbers of bacteria falling onto a plate which do not develop into countable colonies because of interference by neighbouring bacteria.

Mann, K. H. (1953). A revision of the British leeches of the family Glossiphoniidae, with a description of *Batracobdella paludosa* (Carena, 1824) a leech new to the British fauna. *Proc. Zool. Soc. Lond.* **123**, 377–391.

Includes keys and descriptions, a consideration of the status of two 'forms' of *Glossiphonia complanata* and habitat notes for all the species.

Marsden-Jones, E. M. (1953). A study of the life-cycle of *Adleria kollari* Hartig, the marble or Devonshire gall. *Trans. R. Ent. Soc. Lond.* **104**, 195–222.

A careful study of the life-history shows that *Adleria kollari* Hartig, is the agamic form of *Andricus circulans* Mayr. Special attention is given to the preference of oviposition sites by the two forms. Includes a revision of the nomenclature by R. B. Benson.

Marshall, S. M., Orr, A. P. & Rees, C. B. (1953). *Calanus finmarchicus* and related forms. *Nature, Lond.* **171**, 1163–1164.

There is some evidence to show that this Copepod forms two distinct species, *C. finmarchicus* and *C. helgolandicus*. Morphological characters are quoted and it is possible that a third species is represented by material collected at Tromso, Norway.

Meallain, S. O. (1951). Fish-pass at Leixlip dam. *J. Dept. Agric. Eire*, **48**, 3–10.

Describes structure and operation of an automatic lock type of fish pass and estimates its efficiency in passing running salmon. Discusses potential use of electronic counting recorders for obtaining detailed information about numbers of fish moving, in relation to season, temperature, tides, etc.

Miles, M. (1953). Studies of British Anthomyiid flies. (V.—The onion fly, *Delia antiqua* (Mg.).) *Bull. Ent. Res.* **44**, 583–588.

Larvae of *D. antiqua* are only distinguishable from those of *D. cilicrura* and *D. tridactyla* by the number of processes of the anterior spiracles. Notes on the habits, and the timing and pattern of attacks on field crops are given.

Miles, P. M. (1953). The capture and marking of migrant insects. *Rep. W. Wales Fld Soc.* **15**, 28–32.

Notes on the construction and use of a light trap.

Moon, H. P. (1953). A re-examination of certain records for the genus *Asellus* (Isopoda) in the British Isles. *Proc. Zool. Soc. Lond.* **123**, 411–417.

Work of Dr Collinge on the genus is discussed, several species and numerous varieties shown to be invalid, and it is maintained that only three species are known from Britain.

Moore, P. G. (1953). A sequential test for randomness. *Biometrika*, **40**, 111–115.

At London, from 1813 to 1857, there was a significant tendency for wet years to be followed by dry years, and vice versa.

Pantin, C. F. A. (1953). On the name of the ground fluke *Fasciola terrestris* O. F. Müller, on *Othelosoma symondsi* Gray, and on the genus *Amblyplana* von Graff. *J. Linn. Soc. (Zool.)*, **42**, 207–218.

Rhynchodemus terrestris should be known as *Microplana terrestris*.

Perry, R. (1953). Some results of bird ringing. *New Biol.* **15**, 43–59.

As the result of bird ringing since 1899, much information has been collected, although only 4 or 5% of all birds ringed are recovered, concerning: range of individuals and geographical races; migration routes and times; rates of migration; physiological changes affecting migrant birds; details of 'drift' in unfavourable weather and of 'aberrant' migration; explanation of oceanic movements of individual sea-birds, and observations concerning the navigational ability of migrating birds; the length of life of wild birds.

Philipson, G. N. (1953). The larva and pupa of *Wormaldia subnigra* McLachlan (Trichoptera: Philopotamidae). *Proc. R. Ent. Soc. Lond.* (A) **28**, 57–62.

Includes a note on tube building and feeding.

Philipson, G. N. (1953). A method of rearing Trichopterous larvae collected from swift-flowing waters. *Proc. R. Ent. Soc. Lond.* (A) **28**, 15–16.

Richards, O. W. (1953). The classification of the Dryinidae (Hym.), with descriptions of new species. *Trans. R. Ent. Soc. Lond.* **104**, 51–70.

Includes a key for the generic identification of the Dryinidae.

Robinson, H. S. (1952). On the behaviour of night-flying insects in the neighbourhood of a bright source of light. *Proc. R. Ent. Soc. Lond.* (A) **27**, 13–21.

Includes a description of an improved light trap.

Salt, G. (1952). Trimorphism in the Ichneumonid parasite *Gelis corruptor*. *Quart. J. Micr. Sci.* **93**, 453–474.

This parasite is strictly polymorphic in the development of the wings. It is shown that female aptery is a sex-limited character and is of genetic origin. On a host providing adequate nourishment macropterous males are produced; meagre nourishment produces the micropterous male. The two forms of the male differ in other morphological characters.

Sellers, W. F. (1953). A critique on the time-factor in biological control. *Bull. Ent. Res.* **44**, 273–289.

The concepts of W. R. Thompson (1951—*Canad. Ent.* **83**, 230–40) and C. P. Clausen (1951—*Econ. Ent.* **44**, 1–9) are compared with the author's experience. The time-lag for development of full effectiveness of an introduced parasite is discussed. There is danger that adoption of Clausen's view may cause premature abandonment of control programmes. The discussion is based on many examples, especially the control of the gipsy moth (*Porthetria dispar*) in the U.S.A.

Short, J. R. T. (1952). The morphology of the head of larval Hymenoptera with special reference to the head of Ichneumonoidea, including a classification of the final instar larvae of the Braconidae. *Trans. R. Ent. Soc. Lond.* **103**, 27–84.

Short, J. R. T. (1953). A grouping by larval characters of some species of the genus *Apanteles* (Hymenoptera: Braconidae). *Bull. Ent. Res.* **44**, 327–332.

Larval characters of 33 (mainly Palaearctic, including many British) species of *Apanteles* examined in relation to the division of the genus, on characters of the adults, into four main groups of species. Larval characters indicate a grouping of species mainly similar to that based on adult characters.

Van Emden, F. I. (1952). On the taxonomy of Rhynchophora larvae: Adelognatha and Alophoninae (Insecta: Coleoptera). *Proc. Zool. Soc. Lond.* **122**, 651–795.

This most important taxonomic work permits the identification of weevil larvae. The usual classification of the adults is not entirely supported by the relationships of larval morphology.

Varley, G. C. & Edwards, R. L. (1953). An Olfactometer for observing the behaviour of small animals. *Nature, Lond.* **171**, 789–790.

Wallace, H. R. (1953). Notes on the biology of *Coranus subapterus* De Geer (Hemiptera: Reduviidae). *Proc. R. Ent. Soc. Lond.* (A) **28**, 100–110.

Mating behaviour and life-history are described. A list of prey is given. Alary polymorphism is discussed and the different wing forms are described. Brief mention of the typical habitats.

Watt, G. (1952). An experiment in marking the grey seal *Halichoerus grypus*. *Nature, Lond.* **169**, 883.

Numbered steel tags have been used. Initial results suggest that this species may travel considerable distances.

Woodward, T. E. (1952). Studies on the reproductive cycle of three species of British Heteroptera, with special reference to the overwintering stages. *Trans. R. Ent. Soc. Lond.* **103**, 171–218.

It is shown that the life-cycles of *Stenodema laevigatum* and *Myrmus miriformis* are univoltine; that of *Notostira erratica* is bivoltine. In this latter species wing length and the length of the second antennal segment indicate morphological differences between the two generations.

3. PARASITES

Armstrong, E. A. (1953). Nidicoles and parasites of the wren. *Irish Nat. J.* **11**, 57–64.

A list of nidicoles (Mammalia, Arachnida, Hymenoptera, Hemiptera, Diptera, Lepidoptera), brood-parasites (*Cuculus canorus*), ectoparasites (Mallophaga, Aphaniptera, Acarina) and endoparasites (helminth worms, protozoa, bacteria) of *Troglodytes troglodytes*.

Arthur, D. R. (1953). The host relationships of *Ixodes hexagonus* Leach in Britain. *Parasitology*, **43**, 227–238.

All stages of this tick were collected from hedgehogs, stoats, foxes, polecats and ferrets, and one or more stages from fifteen other mammals. Hedgehogs carried most ticks in spring and autumn. The author summarizes the information about the distribution of the tick on its various hosts (including man) and shows that the tick seems to be less common in the north of Britain.

Arthur, D. R. & Thompson, G. B. (1953). Records of ticks collected from birds in the British Isles. *Ann. Mag. Nat. Hist.* (12) **6**, 797–800.

Nine species of tick from 22 species of bird, giving date, site of attachment, numbers, and stages found.

Ash, J. (1952). Records of Hippoboscidae (Dipt.) from Berkshire and Co. Durham in 1950, with notes on their bionomics. *Ent. Mon. Mag.* **88**, 25–30.

A survey of the occurrence of *Ornithomyia avicularia* and *O. fringillina* on birds of 13 species that were systematically trapped in Berkshire during 1949–50. Most flies were found in July–August, and the usual number per bird was one to five. Females of *O. avicularia* and males of *O. fringillina* predominated. Rearing experiments indicated that there is one generation a year. No puparia were found in plumage; a few were found in nests. Experiments on the marking and transfer of parasites are described.

Ash, J. (1952). Siphonaptera bred from birds' nests. *Ent. Mon. Mag.* **88**, 217–222.

Nearly 4000 fleas of five species were bred from 192 nests, mostly from Berkshire, in 1950. Populations of *Ceratophyllus gallinae*, *C. garei* and *Dasypsyllus gallinulae* showed a significant excess of females. There was a significant association between flea species and nest situation.

Barnes, H. (1953). An effect of parasitism on *Balanus balanus* (L.) da Costa. *Nature, Lond.* **172**, 128.

Recent observations suggest that parasitism may not result in complete castration but only in non-liberation of the nauplii.

Broom, J. C. & Gibson, E. A. (1953). Infection rates of *Rattus norvegicus* with *Leptospira icterohaemorrhagiae* in Great Britain. I. A rural area in Carmarthenshire, Wales. *J. Hyg., Camb.*, **51**, 416–425.

At least 23 % of a sample of 357 rats were infected but no cases of Weil's disease in man or cattle are known to have occurred in this area.

Corbet, G. R. (1953). A flat-fly marking experiment. *Fair Isle Bird Obs. Bull.* **12**, 45–48.

The results of marking over 400 *Ornithomyia fringillina*: just under 10 % were recovered; half the birds carrying marked flies still carried them when retrapped. Some flies were recaptured on different hosts from those on which they were released.

David, W. A. L. & Gardiner, B. O. C. (1952). Laboratory breeding of *Pieris brassicae* L. and *Apanteles glomeratus* L. *Proc. R. Ent. Soc. Lond.* (A) **27**, 54–56.

Dawes, B. (1952). Trematode life-cycle enacted in a London pond. *Nature, Lond.* **170**, 72–73.

The definitive hosts of *Diplostomum spathaceum* are various species of gulls. The snail *Limnaea pereger* and the three-spined stickleback are intermediate hosts. The cercaria of the species is a severe pathogen of a number of species of fish.

Green, J. (1952). A Coccidian infecting *Cylindronotus laevioctostriatus* (Goeze) (Col., Tenebrionidae). *Ent. Mon. Mag.* **88**, 207–208.

Oocysts of a species of *Adelina* as yet not separable from *A. tenebrionis* were abundant in the fat body of adults of this beetle in Surrey. When the sporocysts were numerous, they were visible as dark brown spots through the terga after the elytra had been removed.

Gresson, R. A. R. (1952). A new species of *Proteocephalus* from *Coregonus pollan* Thompson. *Irish Nat. J.* **10**, 308–309.

P. pollanicola, a species new to science (named but not described!), is a cestode parasite from the Lough Neagh pollan.

Lees, E. (1953). Life-history of *Gorgoderina vitelliloba* (Olsson). *Nature, Lond.* **171**, 485.

Establishes that the metacercarial hosts are the tadpoles of *Rana temporaria*.

Miles, M. (1952). Parallel diapause in a host insect and its parasite. *Ent. Mon. Mag.* **88**, 63.

Erioischia brassicae usually produces three to four generations a year and its Cynipoid parasite, *Trybliographa rapae*, emerges some time after peak emergence of the host. When the emergence of an adult of *Erioischia brassicae* from puparia collected in October 1949 was delayed until May 1951, that of an adult of *Trybliographa rapae* was delayed until August 1951.

Richards, O. W. (1952). Some records of British Ichneumonidae cyclopneusticae (Hym.). *Ent. Mon. Mag.* **88**, 102.

A list of species, including four new to Britain, mostly taken on a clump of bamboo at Slough, Bucks., in August–September 1933, 1934 and 1938.

Simmonds, F. J. (1953). Inter-relationships of the parasites of the frit-fly, *Oscinella frit* (L.), in eastern North America. *Bull. Ent. Res.* **44**, 387–393.

An investigation undertaken to obtain biological control agents of potential use if introduced into England. Studies the extent and importance of competition amongst larval and pupal parasites of the frit-fly. There appears to be little interference between the various species in the parasite complex.

Smit, F. G. A. M. (1953). The presence in Scotland of *Tarsopsylla octodecimdentata* (Kol.), a flea hitherto unrecorded from the British Isles. *Scot. Nat.* **65**, 5–10.

Two nineteenth-century records from Perthshire of a monoxenous flea of *Sciurus vulgaris* now published for the first time.

Stoker, M. G. P. & Miles, J. A. R. (1953). Studies on the causative agent of an epizootic amongst Manx shearwaters (*Puffinus p. puffinus*). *J. Hyg., Camb.* **51**, 195–202.

Evidence suggests that the virus disease which causes severe blisters in September cannot be classified in any of the known virus groups.

Thompson, G. B. (1953). Notes on ectoparasites. *Rep. Skokholm Bird Obs.* **1952**, 36–37.

Notes on *Ceratophyllus borealis* and *Echidnophaga gallinaceus*, both fleas.

Thompson, G. B. (1953). Contributions towards a study of the ectoparasites of British birds and mammals.—No. 1. *Ann. Mag. Nat. Hist.* (12) **6**, 401–425.

Instructions for collection and preservation of all groups. Descriptions, history, distribution, life-history, effect on host, and parasites of two Diptera Hippoboscidae: *Crataerina pallida* and *Stenepteryx hirundinis*, parasites on the Swift and House-martin respectively.

Thompson, G. R. (1952). A record of *Echidnophaga gallinaceus* (Westwood) (Siphonaptera) from Skokholm Island. *Ent. Mon. Mag.* **88**, 281.

This flea, which was taken on an adult white wagtail (*Motacilla alba*), is here recorded for the first time from the British Isles.

Woodroffe, G. E. (1953). *Actia antennalis* (Rond.) (Dipt., Larvaevoridae) bred from larvae of *Monopis rusticella* (Clerck) (Lep., Tineidae). *Ent. Mon. Mag.* **89**, 11.

The host of this fly was hitherto unknown.

4. FOOD AND FOOD HABITS

Benson, R. B. (1953). A new British *Nematus* (Hym., Tenthredinidae) attacking black-currant. *Ent. Mon. Mag.* **89**, 60–63.

Nematus olfaciens n.sp. attacks *Ribes nigrum*, *R. rubrum* and *R. uva-cristata* in Dundee and Gloucestershire.

Brian, M. V. & Brian, A. D. (1952). The wasp, *Vespula sylvestris* Scopoli: feeding, foraging and colony development. *Trans. R. Ent. Soc. Lond.* **103**, 1–26.

Nest development and brood sequences in a number of nests are described. A few aspects of flesh-feeding are considered, together with role of sugary liquids in the economy of this species. A study of foraging workers is aided by observations on marked individuals.

Conder, P. J. (1953). Some individual feeding habits of gulls breeding on Skokholm. *Rep. Skokholm Bird Obs.* **1952**, 30–34.

Food and feeding habits of *Larus argentatus*, *L. fuscus* and *L. marinus*; foods discussed include limpets, corn, eggs, other birds and ants.

Cott, H. B. (1953). The palatability of the eggs of birds: illustrated by experiments on the food preferences of the ferret (*Putorius furo*) and cat (*Felis catus*); with notes on other egg-eating carnivora. *Proc. Zool. Soc. Lond.* **123**, 123–141.

Results with these predators are similar to those obtained previously with other animals.

Crowcroft, P. (1952). Refection in the common shrew. *Nature, Lond.* **170**, 627.

The habit is described from observations made on juveniles and adults of both sexes of *Sorex araneus*.

Davies, M. J. (1953). The contents of the crops of some British Carabid beetles. *Ent. Mon. Mag.* **89**, 18–23.

A preliminary qualitative examination was made of the crop contents of 366 adult Carabids representing eighty-four species in sixteen tribes. Fairly clear-cut food preferences were found; eight genera were carnivorous, two herbivorous, seven liquid feeders, probably carnivorous, and three mixed feeders, probably scavengers.

Duffy, E. A. J. (1953). Lead cable severely damaged by *Ptinus tectus* Boieldieu (Coleoptera, Ptinidae). *Bull. Ent. Res.* **44**, 83–84.

Larvae, feeding on food scraps discarded in the centre of a wooden cable drum in Kent, bored into lead-sheathed cable in order to pupate.

Fincher, F. (1953). Some notes on the food of birds. *W. Midland Bird Rep.* **18**, 6–9.

Observations on the food taken by 39 species in one wood.

Gillham, M. E. (1953). The distribution of seeds by gulls. *Rep. Skokholm Bird Obs.* **1952**, 34–35.

The breeding gulls of the Pembrokeshire island as a biotic factor in plant distribution.

Green, J. (1952). The food of *Typhaea stercorea* (L.) (Col., Mycetophagidae). *Ent. Mon. Mag.* **88**, 62.

Fungal hyphae were present in the gut contents of five adults, four contained also decayed green plant matter, and two, fungal spores. Sporonts of a septate gregarine protozoan were found in the mid-gut of one.

H[arrison], J. W. H. (1951). The rose leaf-cutter bee (*Megachile circumcincta*) and the leaves of the common convolvulus. *Vasculum* (*sub.*), **36**, 29.

Calystegia sepium attacked by the bee.

Hayden, J. & Kirkby, P. (1953). Observations on bats in the Bishop's Stortford area. *Starfish*, **6**, 8–13.

Includes notes on the food of *Pipistrellus pipistrellus* and on the habits of several other species.

Hill, A. R. (1952). A survey of insects associated with cultivated raspberries in the east of Scotland. *Ent. Mon. Mag.* **88**, 51–62.

Observations on seasonal occurrence, abundance and economic importance of 137 species found on cultivated raspberries, mainly in Angus and East Perthshire and in limited surveys of wild raspberries and wild bramble (*Rubus fruticosus*), including three Mirids recorded from Scotland for the first time. Only *Byturus tomentosus*, *Incurvaria rubiella*, *Otiorrhynchus singularis* and *Lygus pabulinus*, with *Amphorophora rubi* and *Doralis idaei*, both of which transmit raspberry virus diseases, are of major economic importance.

Hodgson, S. B. (1953). Insects at the flowers of orchids. *Entomologist*, **86**, 165.

The moths *Procris geryon* and *Odezia atrata* at pyramidal orchid, and the butterflies *Ochlodes venata* at fragrant orchid, and *Vanessa io* at spotted orchid in Hertfordshire.

Laurence, B. R. (1952). Observations on *Hydrellia* (*Hydropota*) *griseola* Fln. (Dipt., Ephydridae). *Ent. Mon. Mag.* **88**, 31–33.

Both sexes feed on small insects trapped in the surface film of puddles, and a list of insects preyed upon is included. Living insects are attacked. Mating also takes place on the water surface.

Laurence, B. R. (1952). The prey of some Empididae and Dolichopodidae (Dipt.) *Ent. Mon. Mag.* **88**, 156–157.

The prey of *Hilara litorea* flying in deep shade under yew trees, mostly comprised Aphids, although Diptera greatly outnumbered Aphids in a suction trap operated in a more open part of the wood. *Myzocallis annulata*, *M. tiliae* and *Metopolophium dirhodium*, which feed on hazel, lime and grass, respectively, comprised 57 % of the prey of *H. litorea*.

Pringsheim, E. G. (1952). On the nutrition of *Ochromonas*. *Quart. J. Micr. Sci.* **93**, 71–96.

Detailed experimental evidence shows the extraordinary nutritional versatility of *Ochromonas*. Although species of this genus possess chlorophyll, they need additional organic substances for nitrogen, independent carbon and energy sources, and certain growth factors.

Q[uick], H. M. (1953). Some feeding habits (Scilly). *Rep. Cornwall Bird Watch. Soc.* **22** (1952), 51.

Brief notes on food and feeding habits of *Saxicola torquata*, *Turdus ericetorum*, *Arenaria interpres*, *Capella gallinago* and *Rallus aquaticus* in the Scilly Isles in 1952.

R——, C. (1953). The foodplants of the moth *Depressaria angelicella* Hb. *Vasculum* (*sub.*), **37**, 22.

Larvae on *Heracleum sphondylium* in Co. Durham.

Smith, K. G. V. (1952). On the prey of two swarms of *Hilara maura* F. (Dipt., Empididae). *Ent. Mon. Mag.* **88**, 38–39.

In general, the prey of a swarm flying over steadily flowing water in an open, sunny situation and that of another over sluggish water with overhanging bushes were representative of the same orders. Chironomids were most frequently taken, followed by Aphids and, in the shady situation, Psychodids.

Stride, G. O. (1953). On the nutrition of *Carpophilus hemipterus* L. (Coleoptera: Nitidulidae). *Trans. R. Ent. Soc. Lond.* **104**, 171–194.

Consists for the most part of a description of experimental work using artificial foods, but does include a method of culturing this Nitidulid.

Weber, A. P., Zwillenberg, L. O. & Van der Laan, P. A. (1952). A predacious amoeboid organism destroying larvae of the potato Root Eelworm and other Nematodes. *Nature, Lond.* **169**, 834–835.

A new species probably belonging to the family Vampyrellidae (Proteomyxa) has been observed to ingest young larvae of *Heterodera rostochiensis* and other larval Nematodes. Included are notes on the life-history.

Woodroffe, G. E. (1952). A note on the food plants of *Coriomeris denticulatus* (Scop.) (Hem., Coreidae). *Ent. Mon. Mag.* **88**, 255.

Nymphs were confined to *Trifolium arvense* in one gravel pit in Buckinghamshire and to *Medicago lupulina* in another, though the adults occurred on many plants in the former; the food plants of this species therefore appear to be more restricted than has been indicated in the literature. *Syromastes rhombeus*, *Megalonotus chiragra*, *Coreus marginatus* and the predator, *Nabis mirmicoides*, were associated with it in both pits.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Alderton, P. (1953). Seagulls on the outskirts of a town in winter. *Starfish*, **6**, 18–20.

Observations on the diurnal routine of a flock of *Larus argentatus* on a playing field at Brighton, Sussex.

Allen, A. A. (1952). *Lathridius norvegicus* A. Strand (Col., Lathrididae) rediscovered: an addition to the British list. *Ent. Mon. Mag.* **88**, 282–283.

This beetle was, with *L. constrictus*, associated with moulds at and near the edges of bark on the recently burnt parts of an old beech in Epping Forest, but the habitat range of *L. constrictus* was found to be rather wider. *Acritus homoeopathicus* and *Micropeplus tesserula* were also present in the same situation.

Allen, A. A. (1953). The Coleoptera of a suburban garden. 5. Clavicornia (Part I). *Ent. Rec.* **65**, 225–231.

A further sixty-six species are dealt with in this part. [See 1951, *Ent. Rec.* **63**, 61–5, 187–190, 256–259; 1952, *ibid.* **64**, 61–63, 92–93 and abstract in 1953, *J. Anim. Ecol.* **22**, 181.]

Arnold, G. A. & Lapworth, H. (1953). Alvecote Pools. *W. Midland Bird Rep.* **19**, 9–14.

List of the birds observed at a group of artificial freshwater pools in north Warwickshire, since 1928.

Bagenal, T. B. (1953). The birds on St Kilda, 1952. *Scot. Nat.* **65**, 19–24.

Not a complete census of the islands, but an attempt to determine the minimum number present. Thirty-six species were seen on a visit of 18 days in July and August.

Baynes, E. S. A. (1952). Report on migrant insects in Ireland for 1951. *Irish Nat. J.* **10**, 247–248.

Notes on three butterflies, six moths and one bee (*Bombus lucorum*).

Baynes, E. S. A. (1952). Insect migration. *Irish Nat. J.* **10**, 301–302.

A reported instance of migration in the bee *Bombus lucorum* is considered to be more likely to have been a mass movement towards an area with a strong honey-flow.

Baynes, E. S. A. (1953). Report on migrant insects in Ireland for 1952. *Irish Nat. J.* **11**, 45–51.

Reports on eleven species of Lepidoptera and one dipteron from seventeen observers.

Blake, A. R. & Mirams, D. R. (1953). Further observations on the birds of the West Bromwich area. *W. Midland Bird Rep.* **19**, 17–22.

A census of breeding birds in an area of 1800 acres, mainly of grassland.

Boyd, J. M. (1953). The sheep population of Hirta, St Kilda, 1952. *Scot. Nat.* **65**, 25–28.

A comprehensive census showed 1114 Soay sheep on the island, to which 107 were transferred from the neighbouring island of Soay in 1932.

Browne, P. W. P. (1953). Bird migration near Dublin, autumn, 1952. *Irish Nat. J.* **11**, 30–33.

Observations on thirty species, mostly passerines, collated from the notes of nine observers.

Collin, J. E. (1952). Notes on some Drosophilidae (Dipt.), including five additional British species, two of them new to science. *Ent. Mon. Mag.* **88**, 197–199.

The new species are *Drosophila forcipata*, which is widely distributed, and *D. acuminata*, from Devon and Cornwall.

Condry, W. M. (1953). Bird-life on the Dovey estuary. *Rep. W. Wales Fld Soc.* **15**, 21–24.

General notes with some ecological data.

Deane, C. D. (1952). The 'black' rat in the north of Ireland. *Irish Nat. J.* **10**, 296–298.

All three colour forms of *Rattus rattus* occur in Belfast. The species also occurs in a few other places in northern Ireland, and has probably never been extinct, as has been reported.

Eason, E. H. (1953). On *Lithobius aulacopus* Latzel, a centipede new to Britain. *Ann. Mag. Nat. Hist.* (12) **6**, 850–854.

Description. In woodland litter near Lake Windermere.

Fincher, F. (1953). Some notes on Orthoptera and Dermaptera in the West Midlands. *Ent. Rec.* **65**, 151–154.

Observations on abundance, habitats and habits, with dates, for three Dermaptera and ten Orthoptera in Worcestershire, Warwickshire, Shropshire, Flint, Gloucestershire and Staffordshire.

Gibson, F. A. (1953). Movements of salmon around Ireland. II. From Baginbun, County Wexford (1949–1951). *Proc. R. Irish Acad.* **55** B, 195–208.

Most of the fish entered rivers within 50 miles of the tagging point, two made long journeys. The average apparent speed of all fish was between 4 and 7 miles per day.

Gibson, J. A. (1952). The birds of Inch Moan, Loch Lomond. *Glasgow & W. Scot. Bird Bull.* **1**, 6–10.

A list of the birds of an island in a freshwater loch, based on visits over a period of ten years.

Gibson, J. A. (1952). Bird notes from Ailsa Craig, 1951 and 1952. *Glasgow & W. Scot. Bird Bull.* **1**, 11–13.

Censuses of breeding birds of this famous bird rock in the Firth of Clyde.

Gibson, J. A. & Baxter, M. M. (1953). The fulmar colonies of Kintyre. *Glasgow & W. Scot. Bird Bull.* **2**, 38.

About 250 birds were nesting at nine or ten colonies and prospecting at two other sites.

Gibson, J. A. & McWilliam, J. M. (1953). Notes on the birds of the Burnt Islands, Kyles of Bute. *Glasgow & W. Scot. Bird Bull.* **2**, 18–19.

Fifteen to sixteen species nest regularly.

Gibson, J. A. & McWilliam, J. M. (1952). Notes on the birds of the Sgat Islands, Loch Fyne. *Glasgow & W. Scot. Bird Bull.* **1**, 2–3.

Twelve species breed on these two small islands at the mouth of a sea-loch.

Goodbody, I. M. (1953). The autumn migration of skylarks in Ireland. *Irish Nat. J.* **11**, 47–50.

Based on the observations of a team of observers over seven years.

Gordon, A. R. (1953). New records of spiders from West Ross. *Scot. Nat.* **65**, 123–124.

Twenty new county records, with habitat notes.

Gotto, R. V. (1952). Copepods new to British waters. *Nature, Lond.*, **170**, 674.

Records from Strangford Lough, Co. Down. New and rare species to these waters are listed together with their host Ascidians.

Green, J. (1953). Orthoptera in Carmarthenshire. *Ent. Mon. Mag.* **89**, 17.

New county records for four species.

Harrison, D. L. (1953). The distribution of bats (Microchiroptera) in Cambridgeshire. *Naturalist*, **1953**, 111–117.

An account of the status of each of the twelve species which have occurred in the county.

Harthan, A. J. (1953). Recent changes in bird life of the Lenches. *W. Midland Bird Rep.* **18**, 10–11.

Notes on changes in the bird population of an agricultural district since 1938.

Hudson, R., Pyman, G. A. & Spencer, R. (1953). Birds in central Chelmsford, 1952. *Rep. Essex Bird Watch. Soc.* **1952**, 33–35.

The result of almost daily observation on the birds of an open space near the centre of Chelmsford. Seventy-four species were noted.

Hunter, W. R. (1953). Notes on the Mollusca of the Garvelloch Islands. *J. Conch.* **23**, 379–386.

Ecology of land snails; effect of borings of *Hiatella* on littoral fauna.

Hutchinson, M. M. (1953). The bird life of Frensham Great Pond, 1947–1952. *Rep. Haslemere Micr. Soc.* **65**, 5–12.

Notes on the birds of a well-known 77-acre water lying on the borders of Surrey and Hampshire.

Hynes, H. B. N. (1952). The Plecoptera of the Isle of Man. *Proc. R. Ent. Soc. Lond.* (A) **27**, 71–76.

Extensive sampling shows that only ten species were taken.

Jenkins, D. (1953). Diurnal migration near Walsall. *W. Midland Bird Rep.* **19**, 14–17.

Observations made on 12 days in September and October 1952.

Leston, D. (1952). A genus and species of Miridae (Hemiptera) new to Britain, with a key and check-list of the British Deraeocorinae Douglas and Scott. *Ent. Mon. Mag.* **88**, 273–276.

The new species is *Alloeotomus gothicus* (Fallén), from Scots pine in Surrey.

Leston, D. (1952). Some Hemiptera from Huntingdonshire. *Ent. Mon. Mag.* **88**, 162.

Eight new records.

Ling, R. T. (1953). The birds of Great Saltee Island, Eire, August, 1952. *Starfish*, **6**, 13–18.

Includes notes on habitat, food and migration.

Lloyd, R. W. (1953). *Platyrrhinus resinosus* (Scop.) (=*latirostris* (F.)) (Col., Anthribidae) in Oxfordshire. *Ent. Mon. Mag.* **89**, 30.

A new county record. The beetles were feeding on the fungus, *Daldinia concentrica*, especially where snails (*Marpessa laminata*) were also feeding on it.

Macdonald, R. (1952). Amphipoda from north Donegal. *Irish Nat. J.* **10**, 275–276.

Thirteen marine species, mostly from rock pools.

McMeeking, J. M. (1953). Starling roosts in the Oxford area, 1950–1952. *Rep. Oxf. Orn. Soc.* **1952**, 14–17.

Notes on starling roosts in Oxfordshire, N. Berks. and W. Bucks.

McMillan, N. F. & Stelfox, A. W. (1952). Survey of Inishtrahull: Part 6. (Report on the Mollusca collected by Messrs. Ranald Macdonald, B.Sc., and D. J. Sullivan.) *Irish Nat. J.* **10**, 232–235.

Notes on five species of slug, seventeen species of land snail and one freshwater mussel from an island off the coast of Donegal.

Massee, A. M. (1952). Additional county records of the new British Mirid, *Alloeotomus gothicus* Fall. (Hem., Miridae). *Ent. Mon. Mag.* **88**, 276.

For Sussex, Kent and Suffolk.

Mitchell, A. F. (1953). Bird notes from inner Dublin. *Irish Nat. J.* **11**, 66–70.

A list of the birds of the 8-acre Botanic Gardens of Trinity College; of 55 species recorded from December 1951 to October 1952, 22 bred.

Murgatroyd, J. H. (1952). Some further spider records. *Ent. Mon. Mag.* **88**, 151.

Additions to the lists for Dorset, Cheshire, Anglesey, Flint and Derbyshire.

Owen, D. F. (1953). The autumn migration of the meadow-pipit and the skylark on the Kirkcudbright coast. *Scot. Nat.* **65**, 101–107.

Observations made on the Solway in September 1952.

Owen, J. A. (1952). *Agabus biguttatus* Ol. (Col., Dytiscidae), *Laccobius atratus* Rottenb. (*scutellaris* Brit. auctt.) (Col., Hydrophilidae) and other water beetles from Rhum, Scotland. *Ent. Mon. Mag.* **88**, 213.

Agabus biguttatus is recorded for the first time from the Western Islands, and *Laccobius atratus* for the first time from Scotland.

Parmenter, L. (1952). Further additions to the list of Agromyzidae (Dipt.) found in Britain. *Ent. Mon. Mag.* **88**, 279–280.

Localities, dates, food plants and world distribution for nineteen species not hitherto recorded from Britain.

Peacey, A. F. (1953). Neuroptera in Gloucestershire. *Ent. Rec.* **65**, 184–185.

A list of twenty-two species, with localities and dates.

Pearson, A. E. G. & Wilkinson, W. (1952). Continuation List of the Coleoptera of Skokholm Island, Pembs. *Ent. Mon. Mag.* **88**, 42–43.

An additional list of aquatic beetles and some plant-feeding species collected during 1951.

P[yman], G. A. (1953). Swallow and house-martin autumn migration inquiry, 1952. *Rep. Essex Bird Watch. Soc.* **1952**, 41–43.

An outline of the main migration routes of *Hirundo rustica* and *Delichon urbica* in Essex in the autumn of 1952.

Rice, C. (1952). The redstart in Wiltshire: Report of an inquiry conducted during 1949–50–51. *Wilts. Arch. Nat. Hist. Mag.* **54**, 327–331.

The number of pairs known to have nested in the county in each year, together with notes on habitat and nest site.

Richards, O. W. (1952). Hymenoptera-Aculeata collected in Anglesea. *Ent. Mon. Mag.* **88**, 142.

An extensive list, giving dates, localities, food plants and habitats.

Ridpath, M. G. (1953). *Saldula opacula* Van Duzee (Hem., Saldidae) from Hertfordshire. *Ent. Mon. Mag.* **89**, 32.

A new county record.

Ruttledge, R. F. (1952). Report on observations of birds at Irish light-stations, 1951. *Irish Nat. J.* **10**, 314–318.

Important data on bird migration.

Ruttledge, R. F. (1953). Report on observations of birds at Irish light-stations, 1952. *Irish Nat. J.* **11**, 99–101.

Ruttledge, R. F. & Williamson, K. (1952). Early arrival of white-fronted geese in Ireland. *Irish Nat. J.* **10**, 263–264.

Anser albifrons arrived in several parts of Ireland in mid-September, a month ahead of the normal time. Weather conditions over the North Atlantic at the time were favourable to a movement of these geese from Greenland.

Sankey, J. H. P. (1953). Further records of British harvest-spiders (Arachnida, Opiliones) with a note on *Nelima fuscifrons* (Simon), possibly new to Britain. *Entomologist*, **86**, 116–117.

Records for eleven species, with some discussion of the range of *Nelima silvatica* and the habitat of *Anelasmocephalus cambridgei*.

Savidge, J. P. (1953). The effect of weather conditions upon animals and plants. *Proc. Lpool Nat. Fld Cl.* **1952**, 9–10.

Notes on the effect of weather on bird migration in a Cheshire district during 1952.

Smith, K. G. V. (1952). On some Diptera from Dublin and Wicklow with notes on several species new to Ireland. *Ent. Mon. Mag.* **88**, 104–106.

Includes sixteen species new to Ireland, with notes on their occurrence and food plants or hosts in England and Scotland.

Southgate, B. J. & Woodroffe, G. E. (1953). Some Hemiptera-Heteroptera recorded for the first time in Buckinghamshire during 1952. *Ent. Mon. Mag.* **89**, 2.

Five species, with habitats, localities and dates.

Stephen, A. C. (1953). Scottish turtle records previous to 1953. *Scot. Nat.* **65**, 108–114.

Two out of the four species stranded from time to time on the British coasts have occurred in Scotland, on ten occasions; five more occurrences are indeterminate. It is suggested that strandings may be correlated with variations in the strength and direction of the North Atlantic drift.

Stevens, C. J. (1953). Some birds of the Bodmin moors. *Rep. Cornwall Bird Watch. Soc.* **22** (1952), 54–57.

Notes on birds seen during three visits in June and July, 1952, divided on a habitat basis.

Stokes, H. G. (1952). Hemiptera-Heteroptera in South Wales. *Ent. Mon. Mag.* **88**, 22.

Includes some thirty new records for Pembrokeshire.

Stokes, H. G. (1952). Hemiptera-Heteroptera new to Wiltshire. *Ent. Mon. Mag.* **88**, 45.

Some forty-five new county records, with dates and localities.

Stuart, D. (1953). Notes on the birds of Bute. *Glasgow & W. Scot. Bird Bull.* **2**, 14–18.

Covering the years 1938–48, and indicating changes in status of the island's birds since the county avifauna was published in 1935.

Thompson, H. (1953). The edible dormouse (*Glis glis* L.) in England, 1902–51. *Proc. Zool. Soc. Lond.* **122**, 1017–1024.

Distribution in Europe and, since its introduction, in Britain. Notes on habits and its insignificant status as a pest are followed by the recommendation that it should not be further introduced.

Tod, K. (1953). The distribution of the Northern Dart, *Agrotis hyperborea* (Zetterstedt), on the mainland of Scotland. *Scot. Nat.* **65**, 11–18.

Notes on the habitats of a very local noctuid moth. Includes an interesting example of the biotic effect of collectors. In the second week in June 1950 'there was hardly one plant of crowberry which had not been disturbed and often torn up by the roots. Not a single pupa was found, and it is very doubtful whether this locality will survive the devastation by collectors.'

Verdcourt, B. (1952). Further records of Bedfordshire Coleoptera. *Ent. Mon. Mag.* **88**, 73–80.

A list of many species, with dates, localities and habitats, and ecological notes on some of the most frequent localities.

Veysey, C. M. (1953). Some notes on Ham sewage farm and its bird life. *Middle-Thames Nat.* **5**, 5–9.

Notes on the birds of a sewage farm on the Berkshire bank of the Thames near Windsor.

Ware, E. H. (1953). Black redstart, 1952–53. *Rep. Devon Bird Watch. Soc.* **25** (1952), 57.

A summary of the migration of *Phoenicurus ochruros* in Devon in the winter of 1952–53.

Went, A. E. J. (1953). Movements of salmon around Ireland. III. From Carnlough, Co. Antrim (1950 and 1951). *Proc. R. Irish Acad.* **55** B, 209–223.

Most of the movement was Northerly to rivers within about 50 miles. Apparent rates of travel lower than in previous experiments.

Williamson, K. (1953). The nature of spring and autumn passage migration through Britain. *Fair Isle Bird Obs. Bull.* **10**, 3–10.

An exposition of the view that passage migration through the British Isles is due largely to the accident of 'drift'.

Williamson, K. (1953). Migration into Britain from the north-west, autumn 1952. *Scot. Nat.* **65**, 65–94.

An important paper applying the recently revived concept of migrational drift to the autumn bird migration into Britain in 1952 from Iceland and Greenland. It is suggested that this migration is simply a down-wind drift.

6. STUDIES ON BEHAVIOUR

Armstrong, E. A. (1951). The nature and function of animal mimesis. *Bull. Anim. Behav.* **9**, 46–58.

Proposes the term mimesis to describe the reproduction by one animal of the instinctive behaviour patterns it perceives performed by another. By reference largely to birds, but also to some mammals, distinguishes this from imitation and analyses the psychological implications of the phenomenon with both inter- and intra-specific releasers. Suggests that mimesis may be an important factor in causing the 'social increment' effect among colonial-nesting birds.

Brian, M. V. (1952). Interaction between ant colonies at an artificial nest site. *Ent. Mon. Mag.* **88**, 84–88.

When colonies of *Myrmica scabrinodis* and *M. rubra* met under a piece of glass placed on a turf bank and covered by a slate, both at first retreated, but as they became more populous owing to the production of sexuals, the former encroached on the territory of the latter. Workers of *scabrinodis*, but not *rubra*, were present there throughout the winter and reoccupied the whole site in spring; this species is also more tenacious during drought. The colony was later driven out by a stronger one of the same species. Nest structures of *scabrinodis* were more elaborate, stronger and more cellular than those of *rubra*.

Cloudsley-Thompson, J. L. (1952). Studies in diurnal rhythms. II. Changes in the physiological responses of the woodlouse *Oniscus asellus* to environmental stimuli. *J. Exp. Biol.* **29**, 295–303.

The diurnal locomotory rhythm, partly endogenous but primarily controlled by light and darkness, is demonstrated. The inter-relations of humidity, carbon dioxide, light and acclimatization are considered. These results are related to the natural behaviour of the animal.

Cloudsley-Thompson, J. L. (1953). The significance of fluctuating temperatures on the physiology and ecology of insects. *Entomologist*, **86**, 183–189.

The average temperature does not give a good measure of the effect of weather conditions on development, since the thermal optimum in fluctuating temperature may differ from the constant temperature optimum. Fluctuating temperatures are normal for many species; they show differing abilities to withstand constant temperature.

Frisch, K. v. (1951). Recent advances in the study of the orientation of the honeybee, being a translation of extracts from three recent papers. *Bull. Anim. Behav.* **9**, 1–33.

Translations by Dr D. Ilse of recent papers in *Die Naturwissenschaften* **1**, 12–23, **2**, 38–43, **5**, 142–48 (1948) and *Experientia* **6**, 210–221 (1950), the last in summary form only. The first paper 'Solved and unsolved problems of bee language' demonstrates and analyses the methods used in communicating information about the location of food supplies by the dancing patterns of foragers on return to the hive. The patterns adopted give information about direction and distance (as measured by flying effort, and taking account therefore of wind direction and force). Direction is indicated in relation to the sun, whether this be obscured or no, and is recorded regardless of enforced flight deviations. Misdirection becomes frequent when light is admitted to the hive during observation of dances on a vertical surface; and this is analysed in the second paper entitled 'The polarization of light from the sky as an orientating factor in the dances of the honeybee', being found to be due to the bees' ability to detect the position of

the sun when only a small section of blue sky is visible to them. In the dark hive, dancing on a vertical comb-face, the bee transposes direction of the sun towards the direction of the pull of gravity. On admitting light a compromise is recorded between this and the position of the sun as ascertained then from the visible sky. By the use of polarizing screens it is demonstrated that the bee is able to use the polarization of sunlight as observed in the sky as a means of orientation. This is further analysed in the third paper 'The sun as a compass in the life of honeybees', where it is shown experimentally that the been can analyse the polarization of the sky's light.

Griffin, O. G. (1952). Bird navigation, with an appendix by Ernst Mayr on German experiments on the orientation of migrating birds. *Biol. Rev.* **27**, 359–400.

Theories based on Coriolis effect, earth's magnetic field and perception of infra-red radiation are discounted and a theory combining random searching with the recognition of familiar landmarks is shown to account for the observed facts. An addendum reports evidence for orientation based on the sun's position and describes experiments in which homing birds transplanted laterally across Europe during the navigation period continued to travel along a route parallel to the original one.

Matthews, G. V. T. (1953). Sun navigation in homing pigeons. *J. Exp. Biol.* **30**, 243–267.

True navigation (i.e. not due to random search for landmarks) only occurs in sunny conditions; when the sky is overcast the birds scatter at random. The sun navigation hypothesis is shown to be consistent with observations. The errors exhibited by experimental animals are analysed (*a*) under normal conditions, (*b*) after release has been delayed so that seasonal changes of the sun's altitude have occurred, and (*c*) after treatment to desynchronize any internal 'chronometer'. The results point to the measurement of longitude on a time basis and latitude by the sun's altitude. Further critical experiments are discussed.

Matthews, G. V. T. (1953). The orientation of untrained pigeons: a dichotomy in the homing process. *J. Exp. Biol.* **30**, 268–276.

The ability to orientate is innate, but that of homing is ill-developed in young birds and varies with experience. Some of the conflicting results in the literature are due to lack of appreciation of this.

Matthews, G. V. T. (1953). Navigation in the Manx Shearwater. *J. Exp. Biol.* **30**, 370–396.

This paper provides the first conclusive evidence for true homing in a wild species. Homing success was dependent upon sunny conditions. The evidence for a sun-navigation hypothesis is strong and experiments are suggested for obtaining details of the mechanism employed.

Popham, E. J. (1952). Observations on the speed of flight of four species of Corixidae (Hem.). *Ent. Mon. Mag.* **88**, 162.

Corixa punctata, *C. distincta*, *C. praeusta* and *C. nigrolineata* flew at speeds of 1·46, 1·28, 1·37 and 1·31 metres per second on a windless day at 20–25° C. Observations on orientation to light and effect of wind are included.

Popham, E. J. (1952). Observations on the behaviour of aquatic insects during the drying up of a small moorland pond. *Ent. Mon. Mag.* **88**, 180–181.

In a mass migration of the Hemiptera and Coleoptera inhabiting a pond which had nearly dried up. Corixids and Coleoptera flew from the surface of the water or the surrounding land, but *Notonecta glauca* mostly flew from the pond surface. Most *Corixa nigrolineata*, *Acilius sulcatus* and *Gyrinus nutator* flew towards the sun. Most insects that flew from the pond surface fell back or landed on the edge, owing to a turning reflex in response to the reflected light. Some 100–150 Corixids were left in the pond.

Popham, E. J. (1953). The influence of temperature and intensity of illumination upon the phototactic responses of Corixidae (Hem.). *Ent. Mon. Mag.* **89**, 1–2.

In an experiment with *Corixa linnei* in an aquarium illuminated from one side, the proportion showing positive phototaxis increased with temperature of the water and the intensity of illumination.

Popham, E. J. (1953). Measurements of the swimming speeds of some of the commoner species of *Corixa* (Hem., Corixidae). *Ent. Mon. Mag.* **89**, 3.

The horizontal velocity of four Corixids in an aquarium increased with the temperature up to 22·5°C. The number of leg beats per minute also increased, but the number of leg strokes per unit distance showed a considerable decrease.

Ribbands, C. R., Kalmus, H. & Nixon, H. L. (1952). New evidence of communication in the honeybee colony. *Nature, Lond.* **170**, 438–440.

Current views and recent work are discussed. New data are made available and it is suggested that honeybees possess a very delicate capacity for distinguishing between different mixtures of 'odours'; this facilitating social coherence and defence of the community.

Thorpe, W. H. (1951). The definition of some terms used in animal behaviour studies. *Bull. Anim. Behav.* **9**, 34–40.

Records the conclusions and disagreements of a conference at Cambridge in July 1949, arranged jointly by the Society for Experimental Biology and the Association for the Study of Animal Behaviour. Definitions are summarized under the headings of the more elementary behaviour patterns, the concept of instinct and that of learning.

Wilkinson, D. H. (1953). The random element in bird 'navigation'. *J. Exp. Biol.* **29**, 532–560.

This paper concerns wild untrained birds. By calculating a relation between probability of return and distances from home using different random search hypotheses, results are obtained which, when compared with experimental results of Griffin and Rüpell, show that random search cannot be excluded as an explanation of the known data. The hypothesis for migratory flight involves a bias due, for example, to the sun's direction.

7. REPORTS OF ORGANIZATIONS

Fair Isle Bird Observatory Trust (1953). *Annual Report, 1952.* Bulletins Nos. 10–12. (17 India Street, Edinburgh; 21*s.* per annum.)

The annual report contains a summary of work done at the observatory on Fair Isle (Shetland) in 1952, including trapping and ringing birds, the collection of ectoparasites, and the study of the biology of the breeding birds. The Bulletins contain a great many notes and papers on bird migration in various parts of Scotland and Ireland, and on ectoparasites collected at Fair Isle.

Watt, G. (1953). Ornithological report on the Farne Islands for 1952. *Trans. Nat. Hist. Soc. Northumb.* **10**, 81–100.

This report was formerly published privately by the Farne Islands Local Committee of the National Trust. The breeding season was, on the whole, good and damage done by gulls was reduced. Nesting eiders have increased in numbers. Eight new species are added to the systematic list of birds recorded for the islands.

Lundy Field Society (1953). *Sixth Annual Report, 1952* (Secretary, L. A. Harvey, University College, Exeter, 2*s.* 6*d.*).

Includes a summary of censuses of nesting sea-birds, a report on bird migration during the year, and a note on eight species of parasite (2 Hippoboscid flies, 4 Mallophaga, 2 ticks) found on nine species of bird.

Temperley, G. W. (1953). Ornithological report for Northumberland and Durham for 1952. *Trans. Nat. Hist. Soc. Northumb.* **10**, 101–152.

Weather condition delayed some of the earlier migrants, but the breeding season was fairly successful and broods reared were larger than in the previous year. Unusual records included a lesser grey shrike (*Lanius minor*), golden mountain thrush (*Turdus dauma*) and Terek sandpiper (*Xenus cinerea*).

THE BRITISH ECOLOGICAL SOCIETY

Founded 1913

CONSTITUTION AND RULES

1. The object of the BRITISH ECOLOGICAL SOCIETY shall be to promote and foster the study of Ecology in its widest sense.

2. The Society shall consist of Ordinary Members, Honorary Members and Associates as defined in these rules.

3. (*a*) Applicants for membership of the Society shall be proposed by one member (from personal knowledge) or by an Officer of the Society (not necessarily with personal knowledge) and seconded by one other member. Such applications shall be made on a form to be supplied by the Honorary Secretaries, and duly filled up and signed by the applicant.

(*b*) Election shall take place either at a General Meeting or at other times by resolution of the Council. A majority of votes in favour shall result in the election of the applicant.

(*c*) The Secretaries may, however, be empowered by the Council to circulate the names of applicants for membership to members of Council by post, and if they receive no intimation of objection within one week, the applicant shall be deemed to be elected.

4. Subscriptions shall be payable in advance and shall be due on 1 January each year. The annual subscription for ordinary membership shall be twenty-five shillings (25*s.*) and for associate membership seven shillings and sixpence (7*s.* 6*d.*). Members who pay a yearly subscription of 25*s.* shall have the right to receive post free EITHER *The Journal of Ecology* OR *The Journal of Animal Ecology*. An annual subscription of 45*s.* shall entitle members to receive post free BOTH of the Journals above named.

5. In addition to receiving one or both of the Journals of the Society, ordinary members shall have the following privileges:

(*a*) To receive on application any other publications of the Society free or at a reduced rate, as the Council may from time to time determine.

(*b*) To have the use on loan, under regulations, of any photographs or lantern slides in the Society's collections, and of books, maps and pamphlets in the Society's Library.

(*c*) To vote in the election of Council and of Officers.

(*d*) To be eligible for service on the Council and its Committees, or as Officers.

6. Associate members shall have the right to attend meetings and excursions, to obtain through the Secretaries such advice and assistance as the Society can afford, to have the use of photographs and the Library, but they shall not have the privileges of ordinary members indicated in 5(*c*) and 5(*d*).

7. Local Natural History Societies may at the discretion of the Council be allowed to subscribe to the Society twenty-five shillings (25*s.*) per annum and shall thereby be entitled to receive a copy of EITHER of the two Journals of the Society, or on payment of forty-five shillings (45*s.*) per annum, to receive BOTH Journals of the Society. In either case they shall also be entitled (*a*) to such advice or assistance as the Society can afford, and (*b*) to send two delegates to the Society's meetings, to have the same privileges as associate members as regards such meetings.

8. (*a*) The Society shall be governed by a Council of not more than twenty-five members, consisting of the officers and sixteen ordinary members of Council.

(*b*) The officers shall consist of the President, two Vice-Presidents, the two Honorary Editors, two Honorary Secretaries, and two Honorary Treasurers.

(*c*) Officers and ordinary members of the Council shall be elected at the Annual Meeting of the Society except as provided under Rule 11.

9. (*a*) Four ordinary members of Council shall be elected each year and shall serve for a period of four years, at the end of which time they shall retire. They shall not be eligible for re-election until the Annual Meeting of the year following their retirement, except as provided under Rule 11.

(*b*) An ordinary member of the Council, when elected an Officer of the Society, shall cease to be an ordinary Council member. Any vacancy thus created shall be filled in the manner prescribed in Rule 11.

(*c*) On expiry of office the retiring Officers shall be eligible for immediate re-election as ordinary members of the Council.

10. (*a*) The President of the Society shall hold office for two years, and it shall be his duty to deliver an address to the Society at the Annual Meeting next after that at which he was elected.

(*b*) One Vice-President shall be elected each year and shall hold office for two years.

(*c*) The two Honorary Editors and the two Honorary Secretaries shall retire at the end of each year but shall be eligible for immediate re-election.

(*d*) The two Honorary Treasurers shall be elected for a period of three years and shall be re-eligible. The Honorary Treasurers shall keep the Society's funds and be responsible for the collection of subscriptions. Their sanction shall be required for the disbursement of the Society's moneys. The financial status and policy of the Society shall be considered each year at the meeting of Council held as soon as practicable after the audit. A financial statement shall be made to the Society at its next meeting. The audited accounts shall be published in the Journals of the Society.

11. (*a*) The Council shall have power to co-opt any ordinary member of the Society to fill vacancies occurring during the year among Council members or officers, the tenure of such co-opted members to terminate at the next Annual Meeting.

(*b*) Members elected at the Annual Meeting to fill such vacancies shall complete the period of service of the Council members (four years) or Vice-President (two years) whose places they have taken. A member elected to fill such a vacancy among the ordinary members of Council, shall, on retirement, be eligible for immediate re-election if his service (co-opted and/or elected) does not exceed two years.

12. If any Council member does not attend at least one meeting of the Council during a year he shall retire at the end of that year, but shall be eligible for re-election. The vacancy thus created shall be subject to the provisions of Rule 11 (*b*).

13. (*a*) At least two weeks before the Annual Meeting the Secretaries shall circulate to all members of the Society, resident in the British Isles, a list of the members of Council including officers, indicating those who retire and adding the names of nominees of the Council to fill the vacancies.

(*b*) Members may propose for ballot at the Annual Meeting the name or names of any duly qualified member or members in place of any or all of the Council's nominees.

14. At the Annual Meeting, after nomination by the Council, persons who have rendered conspicuous service to the subject of Ecology may be elected honorary members of the Society. Such honorary members shall receive free either or both Journals of the Society as the Council may determine, and shall also have the other privileges of ordinary members of the Society.

15. The Annual Meeting shall be held in December or in the following January. At least one other meeting shall be held in the year. Further meetings and excursions may be held at such times and places as the Council may from time to time determine.

16. At the Annual Meeting the members of the Society present shall ballot for Officers and Council and consider any other business brought before them by the Council or by any members, of which four weeks' notice in writing has been given to the Secretaries.

17. Alterations of the rules shall be made only at the Annual Meeting and require six weeks' notice in writing to the Secretaries, and a majority of two-thirds of the members present and voting.

18. At any meeting of the Society the Chairman shall decide as to procedure and the order of business. It shall be within the Chairman's discretion to admit communications or other business, other than alterations to the rules, not included in the programme.

19. A Meeting of the Council to consider the Annual Report shall be held shortly before the Annual Meeting.

20. Members desiring to present communications at any meeting must give due notice to the Secretaries, stating the nature of the communication and the time required.

21. The Society shall issue two Journals, *The Journal of Ecology*, and *The Journal of Animal Ecology*.

22. The subscription price of each Journal to others than members of the Society shall be as determined by the Council.

23. No member shall be entitled to receive the Journals of the Society whilst his subscription is in arrear.

[The above rules were adopted at the Annual General Meeting of the British Ecological Society at Sheffield on 6 January 1954.]

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1953

Income

	£ s. d.	£ s. d.
Subscriptions received, including arrears, and *less* payments in advance:		
Members taking *Journal of Ecology* only	544 19 10	
Members taking *Journal of Animal Ecology* only ...	290 0 3	
Members taking both Journals	305 19 6	
Associates	3 15 0	
		1144 14 7
Interest on Investments	102 0 0	
Interest on Deposit Account	11 13 1	
Interest on P.O. Savings Bank Account	91 0 0	
		204 13 1
Journal of Ecology: Sales *less* costs		38 13 3
Journal of Ecology, Index to vols. 1–20: Sales	11 2 0	
Less costs ...	1 7 7	
		9 14 5
Watson's Census Catalogue of British Lichens: Sales ...		1 5 0
		£1399 0 4

Journal of Ecology:	
Sales: Current volume 41	1547 15 4
Back volumes and parts	738 3 11
Reprints of papers	127 14 8
Advertising Space	11 6 9
	£2425 0 8
Journal of Animal Ecology:	
Sales: Current volume 22	998 4 7
Back volumes and parts	715 12 8
Reprints of papers	82 9 8
	1796 6 11
Balance (see above, as Expenditure)	466 7 1

Expenditure

	£ s. d.	£ s. d.
Working Expenses:		
Expenses of meetings	30 5 5	
Clerical assistance	27 4 0	
Audit Fee	12 12 0	
Postages, etc.	11 2 0	
Printing and Stationery	7 11 3	
Travelling	5 11 1	
Addressograph stencils, etc.	2 19 11	
Telephone	2 8 3	
Bank charges	1 6	
		99 15 5
Grants:		
Freshwater Biological Association	10 0 0	
Watson's Census Catalogue of British Lichens ...	140 0 0	
		150 0 0
Journal of Animal Ecology: Costs *less* sales		466 7 1
Biological Flora of British Isles: Costs	118 5 5	
Less sales	9 0 10	
		109 4 7
		825 7 1
Balance—Surplus for Year		573 13 3
		£1399 0 4

Journal of Ecology:	
Costs: Printing, Paper, Blocks and Binding	2012 18 1
Publishers' Commission	287 4 2
Carriage, etc.	75 8 7
Insurance of Stock	5 8 11
Editor's expenses	4 4 8
Miscellaneous expenses	1 3 0
	2386 7 5
Balance (see above, as Income)	38 13 3
	£2425 0 8
Journal of Animal Ecology:	
Costs: Printing, Paper, Blocks and Binding:	
Vol. 14 (500 extra copies)	267 10 0
Current volume 22	1696 8 3
Publishers' Commission	209 0 9
Carriage, etc.	52 3 0
Fee for checking references	20 0 0
Insurance of Stock	14 3 10
Editor's expenses	3 8 2
	£2262 14 0

BALANCE SHEET AT 31 DECEMBER 1953

Assets

	£ s. d.	£ s. d.
Cash in hand at Westminster Bank:		
Current Account	592 13 7	
Deposit Account	500 0 0	
		1092 13 7
Post Office Savings Bank Account		3731 5 10
Sundry payments in advance		1 4 4
Publishing Account due from Cambridge University Press:		
Journal of Animal Ecology		973 2 8
Investments at Cost:		
£1200 of 3½% War Loan Stock	1230 4 1	
£700 of 3% Savings Bonds 1960/70	700 0 0	
£300 of 3% Savings Bonds 1965/75	300 0 0	
£1000 of 3% Redemption Stock 1986/96	1005 18 6	
		3236 2 7
		£9034 9 0

{VICTOR S. SUMMERHAYES
C. E. HUBBARD
Hon. Treasurers

Liabilities

	£ s. d.	£ s. d.
Members' Subscriptions, prepaid for 1954/57		31 17 5
Library Fund		1 5 0
Printing Accounts owing to Cambridge University Press:		
Journal of Animal Ecology	808 4 4	
Biological Flora	11 4 6	
		819 8 10
Sundry Accounts owing:		
Journal of Animal Ecology	23 8 2	
Journal of Ecology	4 4 8	
Sundry working expenses	6 13 4	
		34 6 2
General Revenue Account—Surplus in hand:		
Balance at 31 December 1952	7573 18 4	
Surplus for the year 1953	573 13 3	
		8147 11 7
		£9034 9 0

We have examined the Balance Sheet and Income and Expenditure Accounts of the British Ecological Society as at the 31st December 1953, set forth above. We have obtained all the information and explanations we have required, and have verified the investments and Balance at Bank. In our opinion the above Balance Sheet is properly drawn up as to exhibit a true and correct view of the state of the Society's affairs, according to the best of our information and the explanations given us, and as shown by the books of the Society.

RYLAND CLIFT & NEAL
Incorporated Accountants

10 ECCLESTON PLACE,
WESTMINSEER, S.W.1
23 *March* 1954

NOTICE TO CONTRIBUTORS

Contributors are asked to study these notes with care in order to save themselves and the editor unnecessary work in the revision of manuscripts.

1. All correspondence should be addressed: **The Editor, Journal of Animal Ecology, The Ferry House, Ambleside, Westmorland.**

2. TEXT. MSS should be typed double-spaced on one side of the paper, leaving top and left-hand margins at least an inch wide. Latin names of genera and species, **but nothing else,** should be underlined. Months of the year should be abbreviated (Jan., Feb., etc.) not indicated by figures. Text-figures are to be referred to as 'Fig. 1' etc.

The *Journal's* conventions regarding cross-headings should be followed, but they should not be used too freely, **nor should headings be underlined.** Only long papers need include a table of contents. The Royal Society's *General notes on the preparation of scientific papers* should be followed on points not mentioned here.

3. LATIN NAMES. Excepting those of British vertebrates, all Latin specific names should be followed by the authority when the name is first mentioned in the text or tables. Names must be verified either from a standard list such as Kloet and Hincks's *Check-List of British Insects* or by submitting the final MS to the experts who have supplied the identifications.

4. REFERENCES should be listed in alphabetical order at the end of the paper in the form:

Vevers, H. G. & Fisher, J. (1938). The 1938 census of gannets (*Sula bassana*) on Ailsa Craig. *J. Anim. Ecol.* **7**, 303–4.

Titles of journals should be abbreviated according to the *World List of Scientific Periodicals*, except that the English usage of capitals for adjectives should be followed. Before the MS is sent in, all references must be verified from the original sources; any reference not personally seen should be marked with an asterisk. **Nothing** except Latin names of genera and species should be underlined, nor should titles of papers or books be put in inverted commas.

5. TABLES should be set out on separate sheets and numbered in arabic numerals. So far as possible sufficient description should be included in the headings to make tables self-explanatory. The layout of tables should be kept as simple as possible; they are not printed 'boxed'.

6. TEXT-FIGURES. Drawings should be in jet-black indian ink, preferably on Bristol board. Shading must consist of lines or dots, not of half-tone washes. If the addition of mechanical stippling or hatching is required the area should be indicated by hatching lightly in blue pencil. Drawings should be arranged or grouped so that after suitable reduction a figure about 5 in. wide results.

Graphs should be drawn on paper ruled in blue or faint grey; axes and graduation marks must be drawn in indian ink.

All lettering, numerals and arrows should be shown lightly in pencil for insertion in uniform style by the blockmaker.

The author's name and the number of the figure should be written on the back of each. Legends for figures should be collected together at the end of the MS.

7. PLATES. Photographs will only be used to illustrate important points which cannot conveniently be shown in any other way. Unmounted, glossy, half-plate prints showing good detail and moderate, but not excessive, contrast, are required. They should be numbered separately from text-figures, and each print should bear on its back the number and the author's name.

8. PROOFS. Page-proofs only will be sent. They should be returned with the least possible delay, and the minimum of essential correction should be made. Authors are requested to pay particular attention to the checking of numerical matter, mathematical formulae, tables and lists of names.

9. REPRINTS. Authors are supplied with 50 reprints gratis. Additional copies may be purchased if ordered when the proofs are returned. Contributors from abroad should order when sending their MSS. Reprints are sent out about a month after publication.